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Seasonal Reproduction And Group Dynamics Of Bushy-tailed Woodrats, Neotoma Cinerea

Graham John Hickling

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SEASONAL REPRODUCTION AND GROUP DYNAMICS OF BUSHY-TAILED WOODRATS, *NEOTOMA CINEREA*

by

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Submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

It has been proposed that bushy-tailed woodrats (Neotoma cinerea) exhibit a harem-polygynous social system (Escherich 1981). I monitored 16 groups of N. cinerea in rocky habitat in the Kananaskis Valley, Alberta, from 1984 through 1986 to determine whether reproduction, growth, group size, and group sex ratio of this species were proximately limited by food abundance. Supplemental food was supplied to 8 groups through 2 successive breeding seasons, and the fed and unmanipulated groups were monitored using mark-recapture techniques. N. cinerea first bred as yearlings, with females producing 1 or 2 litters each season. Food addition resulted in early breeding ($p<0.02$), an increased number of litters per season ($p<0.05$), and an increased litter size at weaning ($p<0.05$). Food addition also increased post-weaning growth ($p<0.0001$) and overwintered body weight ($p<0.005$). These results support the hypothesis that food is a proximate limit to female reproduction and growth. The average group of N. cinerea consisted of a single overwintered male and 2 or 3 overwintered females with associated juveniles. Group sex ratio was female biased on the majority of areas (69% in 1985; 88% in 1986). Most females (71%) but few males (17%) were born on the area on which they subsequently bred. The variable components of N. cinerea social organization were male ranging behaviour and female group size. The majority of overwintered males (54%) were only trapped on a single rocky outcrop. The remaining males roamed among adjacent outcrops (17%), or were non-territorial transients (29%). These alternate ranging tactics were related to differences in age and body weight

among males. Each overwintered female was closely associated with a single rock outcrop. Female group size was positively correlated (r_s=0.62, $p<0.02$) with the length of these outcrops. However, neither group size nor group sex ratio were influenced by food addition. These results do not support the hypothesis that food is a proximate limit to the level of polygyny exhibited by *N. cinerea*.

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CHAPTER ONE - GENERAL INTRODUCTION

The relative ability to obtain nutritional resources from the environment has a greater influence on the reproductive success of females than males (Trivers 1972). Reproductive success of a female is usually limited by the rate at which she can convert resources into offspring, whereas a male's success is usually limited by the rate at which he can find and mate with females (Krebs and Davies 1984). For mammals, this asymmetry arises because gestation and lactation force females to make a larger investment in their offspring than do males (Trivers 1972).

The resources required by females are often patchily distributed. Rubenstein and Wrangham (1986) have suggested that sociality has arisen within some mammalian species as a consequence of the grouping of females within these patches of abundant resources. Groups of females represent a patchy resource for males, and variation in male social behaviour may relate to differing patterns of female dispersion (Erlinge and Sandell 1986; Wrangham 1982). Thus, ecological factors which influence female dispersion may play a fundamental role in determining variation in mammalian social organization.

Several authors have related variation in mammalian social organization to differences in ecology among species (Crook et al. 1976; Emlen and Oring 1977; Orians 1969). When the distribution of physical resources is heterogeneous, Emlen and Oring (1977) hypothesized that a territorial male may exclude other males from a habitat patch and thereby monopolize a group of breeding females (this is termed "resource defence polygyny"). Wittenberger (1980) proposed

an optimal group size model, which predicts that variation in habitat quality will result in variation in the level of polygyny that develops on these habitat patches. The model assumes that the decision of a female to remain in a polygynously-mating group involves a trade-off between the benefits of access to the group's resources and the costs of competition for resources among members of the group. The model predicts, therefore, that levels of polygyny may be influenced by the abundance of certain "critical" resources (sensu Emlen and Oring 1977) such as den sites or food.

The majority of studies which have considered these and other hypotheses of mammalian social organization have used a comparative approach to assess the relationship between sociality and ecology (e.g. Barash 1974; Clutton-Brock 1974; Dobson 1984; Jarman 1974; Michener 1983; Waser 1981). These studies have related variation in social organization among a number of species to one or more environmental variables. Less information is available on the relationship between the ecology of a single species and variation in its social organization (e.g. Cowan and Garson 1985; Erlinge and Sandell 1986; Getz and Carter 1980; Hoeck et al. 1982), in part because species exhibiting variable social organization are relatively uncommon (Jarman 1982). The study of species which do exhibit such variation provides opportunities to experimentally test hypotheses erected to explain the evolution of interspecific variation in sociality.

Seasonal restrictions in the quantity or quality of available food have been proposed as important limits to the density of small mammal populations (e.g. Hansson 1979; White 1978). Krebs and Davies

(1984) suggest that such hypotheses are best tested by manipulative field experiments, and a number of recent studies have involved the experimental manipulation of food resources available to natural populations of small mammals (Briggs 1986; Cole and Batzli 1978; Desy and Thompson 1983; Dobson and Kjelgaard 1985; Ford and Pitelka 1984; Gilbert and Krebs 1981; Mares et al. 1976, 1982; Sullivan and Sullivan 1982; Sullivan et al. 1983; Young and Stout 1986; and others). These studies have demonstrated that food availability can have a proximate effect on a variety of demographic parameters. Boutin (1984) suggested that the usual response of a small mammal population to supplemental food could be summarized as a two- to three-fold increase in density through immigration, early breeding, and in some cases, improved survival.

Food addition has been shown to have a greater influence on the population dynamics of females than males in several species of small mammal (Fordham 1971; Hansen and Batzli 1978; Taitt 1981; Taitt and Krebs 1983). These studies support the hypothesis that different factors may limit the relative numbers of males and females in a population (Krebs 1985; Petticrew and Sadleir 1974). Furthermore, differential response of the sexes to food addition suggests that it may be possible to manipulate the social organization of some species through experimental changes in resource levels. Although mating systems have been altered in avian populations by increasing nest sites or food availability (e.g. Ewald and Rohwer 1982; Pleszczynska and Hansell 1980), this experimental approach has not been used to manipulate the social organization of a mammalian species.

In this study, I determined the effect of food availability on seasonal reproduction and group dynamics of bushy-tailed woodrats (Neotoma cinerea Ord). N. cinerea is a non-hibernating, nocturnal, cricetid rodent found in montane areas of western North America (Plate 1a). Bushy-tailed woodrats gather sticks and other dry vegetation to form dens in rock crevices or caves; each den is rarely occupied by more than 1 adult (Escherich 1981). Large quantities of green vegetation may be stored in the den as a food cache (Finley 1958; Salt and Clarke 1979). N. cinerea is a generalist herbivore (Finley 1958) and exhibits seasonal reproduction. Females are seasonally polyestrous, and neither sex breeds in the year of their birth (Egoscue 1962). N. cinerea is the largest, and most boreal, member of the genus. I will henceforth refer to N. cinerea as the "bushy-tail" (after Escherich 1981), while "woodrat" will be used as a generic term for Neotoma.

Escherich (1981) reported that male bushy-tails in the Sierra Nevada Mountains maintained a harem-based mating system and implied that this pattern of social organization was a consequence of resource defense polygyny. Finley (1958) and Escherich (1981) suggested that the main resource limiting the number of resident bushy-tails in patchy habitat was the availability of den sites, although no quantitative evidence was presented in support of this hypothesis. I designed a study to investigate an alternative explanation for population regulation in this species; that the number of bushy-tails on a habitat patch is proximately limited by food. I expected that competition for food would be particularly evident during winter, when forage availability is low (Porter and McClure 1984), or during

reproduction, when female nutritional requirements are elevated (Randolph et al. 1977).

Preliminary observations in the Kananaskis Valley of the Canadian Rocky Mountains during 1984 indicated that bushy-tails formed a variety of social groupings in this area, ranging from male-female pairs to small groups of resident adults with associated juveniles. Settlements of bushy-tails were closely associated with rocky habitat, which ranged from caves and isolated rock outcrops to more extensive areas of talus slope and rock escarpment (Plate 1b). These rock outcrops were widely separated and were in many ways analogous to "islands" of suitable habitat (c.f. Hoeck 1982). MacArthur and Wilson (1967) suggested that "islands provide the necessary replications in natural 'experiments' by which evolutionary hypotheses can be tested". I provided supplemental food to a number of these bushy-tail settlements during two successive breeding seasons to determine whether food abundance limited the number of female bushy-tails which bred on each patch of habitat.

I have not presented an extensive description of the general biology of bushy-tails in this thesis. Finley's (1958) monograph on the woodrats of Colorado and Escherich's (1981) account of the social biology of bushy-tails provide lengthy descriptions of the natural history of this species. I intend that this study complement these descriptive accounts by emphasising a more quantitative approach.

This thesis is divided into 5 Chapters.

Chapter 2 provides a description of my study area and outlines the methods used.

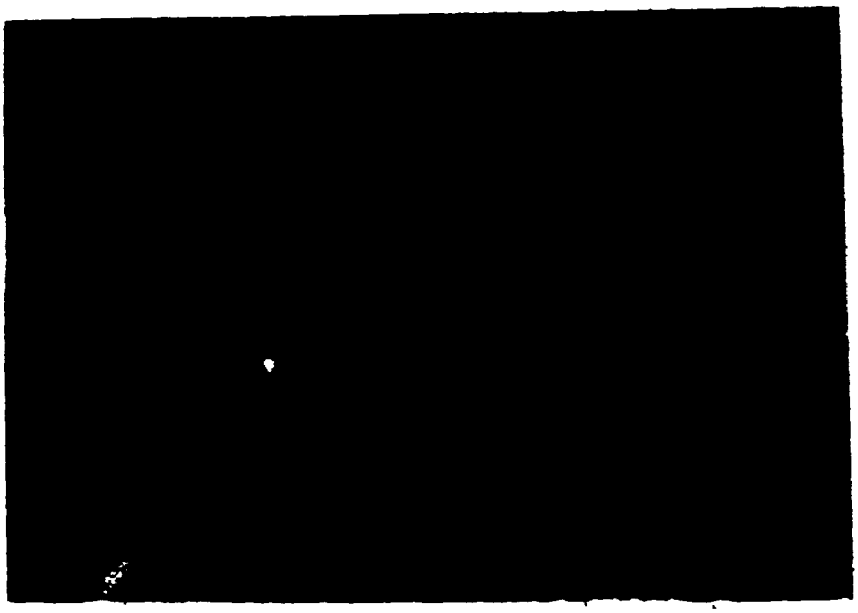
Chapter 3 describes the reproductive ecology of bushy-tails, and tests the hypothesis that seasonal changes in food abundance limit reproduction and growth of bushy-tails. A prediction of this hypothesis is that the experimental addition of food would increase the reproductive output and growth of this species. Confirmation of this prediction would demonstrate that food acts as a proximate rather than an ultimate limit to reproduction and growth, which is an implicit assumption of my suggestion that group size may be proximately limited by the abundance of food.

Chapter 4 relates group dynamics of bushy-tails in the Kananaskis Valley to their social organization. Chapter 4 is based on the following hypotheses; first, that bushy-tails exhibit resource defense polygyny (sensu Emlen and Oring 1977) and second, that the observed level of polygyny would increase on areas supplied with supplemental food. Confirmation of this latter hypothesis would demonstrate that the social organization of this species is proximately controlled by the distribution and abundance of food.

Chapter 5 summarizes the conclusions of my study, and discusses their relevance to our understanding of the population dynamics of N. cinerea.

PLATE I.

a) An adult female bushy-tail. b) Kel's Bluff, an example of the patches of rocky habitat in the Kananaskis Valley that were live-trapped during this study.

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CHAPTER TWO - GENERAL METHODS

2.1. Study area

Small groups of bushy-tails were studied in patches of rocky habitat in the lower Kananaskis Valley (51°N, 115°W) in the Canadian Rocky Mountains, Alberta, from 1984 through 1986. The study was confined to the Kananaskis River drainage. between the northern boundary of Peter Lougheed Provincial Park and Sibbald Creek (Figure 1). All study populations were located in the subalpine vegetation zone (Ogilvie 1969) at elevations ranging between 1450 m and 1800 m.

Mature forest stands in the valley were composed primarily of white spruce (Picea glauca) and Engelmann spruce (Picea engelmannii), with subalpine fir (Abies lasiocarpa) and alpine larch (Larix lyallii) at higher elevations. Post-fire forests at low elevation were dominated by lodgepole pine (Pinus contorta) and trembling aspen (Populus tremuloides) (Rowe 1972). On steep, unstable slopes the forest canopy was usually replaced by mixed shrubs (Salix sp., Betula glandulosa, Ribes sp., Shepherdia canadensis, Potentilla fruticosa, Juniperus communis and Arctostaphylos uva-ursi) and a variety of forbs and grasses. Millar et al. (1985) described 14 main habitat classes in which small mammals were found in the Kananaskis Valley; of these, bushy-tails were closely associated with the talus and cliff habitat class.

The mammalian fauna of the area is diverse, due in part to the changing patterns of species distribution associated with the onset of dryer, warmer climates following the last period of glaciation

(Hoffman and Jones 1970). Millar et al. (1985) identified 25 species of small mammal during a 3-year trapping survey of the Kananaskis Valley. Of these, the species most commonly observed in the vicinity of bushy-tail habitat were least chipmunk (Eutamius minimus), golden-mantled ground squirrel (Spermophilus lateralis), red squirrel (Tamiasciurus hudsonicus), pika (Ochotona princeps), deermouse (Peromyscus maniculatus), and red-backed vole (Clethrionomys gapperi). Potential predators included pine marten (Martes americana) and long-tailed weasel (Mustela frenata).

Environmental conditions in the Valley were highly seasonal; mean monthly temperatures typically range from 14°C in July through -10°C in January, with a mean annual precipitation of 360 mm rain and 290 mm snow (Environment Canada 1983). Warm westerly 'Chinook' winds result in complete removal of snow-cover at low elevations at irregular intervals during some winters.

2.2. Trapping techniques

I used live-trapping and kill-trapping to monitor the seasonal ecology and group dynamics of bushy-tails on my study area. Mark-recapture live-trapping allowed me to monitor seasonal patterns of reproduction, growth, home range size, and group composition. Necropsy of kill-trapped bushy-tails provided information on diet (from stomach contents), endogenous energy reserves, and additional information regarding seasonal reproduction.

2.2.1. Trapping areas.

Preliminary trapping during 1984 was used to locate 16 discrete patches of rocky habitat that were inhabited by bushy-tails. These areas were ranked in order of horizontal length of exposed rock, as measured from aerial photographs provided by the Alberta Ministry of Energy and Natural Resources (series 82-176C, scale 1:20000). Length, rather than plan area, was measured from the aerial photographs because the slope of the trapping areas varied widely in the rugged terrain of the Kananaskis Valley. The 16 areas were divided into 8 pairs in order of length. One area from each pair was then randomly selected to receive supplemental food; these are termed "fed" areas. The other area in each pair remained unmanipulated; these are termed "control" areas.

Control areas were live-trapped at 3-week intervals from spring through fall in 1985 and 1986, but were otherwise undisturbed. Fed areas were live-trapped in a similar manner, but were provided with supplemental food from May 1985 through September 1986. Locations of control and fed areas are given in Figure 1., and other relevant information is given for each area in Appendix I. Several other settlements of bushy-tails in the Kananaskis Valley were live-trapped during either 1985 or 1986 to obtain additional growth and home-range data.

Five "removal" areas were intensively kill-trapped during 1984, and subsequently live-trapped at 3-week intervals from spring through fall in 1985 and 1986 to monitor the re-establishment of bushy-tails in the vacant habitat. Additional kill-trapping was conducted during 1985 and 1986 to obtain carcasses for necropsy. Kill-trapping was

conducted in areas located several kilometres from the nearest live-trapping area.

2.2.2. Live-trapping.

Live-trapping was conducted using Tomahawk® collapsible traps (No. 502) with a 12 mm x 25 mm mesh size. Traps were baited in the evening with peanut butter and apple, and checked early the next morning to reduce the risk of bushy-tails suffering heat stress in the traps. Bushy-tails were sensitive to hypothermia if they became wet, so care was taken to place traps in sheltered areas.

Given the rugged terrain in which bushy-tails were found, I was unable to employ a grid arrangement of traps. Traps were located on transects that ran along the base of bluffs, up ledges, or along the top of ridges. Traps were usually spaced at about 20 m intervals, with additional traps placed wherever fresh urine markings indicated the presence of an occupied den. Trap density was increased in response to the appearance of juvenile bushy-tails on the trapping areas as the breeding season progressed. Each time an area was trapped, an additional trap was placed within a few metres of any trap which had previously captured a bushy-tail, unless an unsprung trap was already present. Thus, at least twice as many traps were set as there were bushy-tails being caught, which ensured that there was a high probability of capturing the resident bushy-tails on each area.

Live-trapping was conducted for several successive days when the areas were first established, and thereafter for one night at 21-day intervals, or as close to 21 days as weather conditions would allow. Bushy-tails have a gestation period of about 30 days (Egoscue 1962)

and a lactation period of about 23 days (pers. obs.). Thus, a 21-day trapping interval was sufficient to monitor patterns of seasonal reproduction. Trapping intervals were sometimes modified to avoid trapping during periods of rain or snow, and live-trapping was discontinued from September 1984 through March 1985, and from November 1985 through March 1986, to avoid trap mortality during the cold winter months.

Live-trapped bushy-tails were tagged in each ear with individually numbered eartags (Monel® No. 1), weighed (nearest 1.0 g) with a Pesola® spring balance, sexed, and classified as juvenile or overwintered on the basis of pelage. Head length (distance from the posterior edge of the supraoccipital crest to the tip of the nose) was measured to the nearest 0.5 mm. Females were classified as perforate or non-perforate on the basis of the vaginal membrane; as not pregnant, in early pregnancy, or in advanced pregnancy by abdominal palpation; and as non-lactating, lactating, regressing or post-breeding on the basis of nipple enlargement. Males were classified as scrotal or non-scrotal on the basis of testes position, and their ventral sebaceous gland was ranked as inactive (0), slightly active (1), moderately active (2), or very active (3), based on the degree to which the ventral fur was matted with glandular secretions. The length and width of the patch of oily fur were also measured (nearest 5.0 mm) and an index of scent gland activity was calculated as the activity rank multiplied by the area of stained fur. The number of visible wounds was recorded.

2.2.3. Kill-trapping and necropsy procedures.

Kill-trapping was conducted using Conibear® traps (No. 110) baited with peanut butter. Kill-trap areas were initially trapped for 2 or 3 successive nights. Some areas were re-trapped later in the same season or during subsequent years. Kill-traps were located in a similar manner to live-traps. Carcasses were necropsied on the day of capture, or frozen until a necropsy could be performed.

During necropsy, I recorded body weight (nearest 1.0 g) and standard measurements (nearest 0.5 mm) for total length, tail length, hind foot length (Anderson 1964) and head length (see 2.2.2). Stomach contents were removed and frozen. The carcass was skinned and the reproductive tract and skull removed. Weight of the reproductive tract (nearest 0.1 g), counts of embryos and placental scars, lengths of embryos (nearest 1.0 mm), and width of nipples (nearest 0.1 mm) were recorded for females. Testes weight (nearest 0.01 g), testes length (nearest 0.1 mm), the presence or absence of sperm in the epididymides and the activity of the ventral sebaceous gland (see 2.2.2.) were recorded for males. Reproductive tracts were fixed in 10% formalin, and later transferred to 70% ethanol for longterm storage.

2.3. Food addition

I used a dispersed pattern of feeding stations, rather than a large amount of food at a centralized location, to reduce the possibility of one bushy-tail restricting the access of other individuals to the food (e.g. Mares et al. 1976; Noyes et al. 1982). Feeding stations were located at 20-30 m intervals among the rock

outcrops. Thus, the number of feeding stations in each area (Appendix I) was approximately proportional to the length of each rock outcrop.

Supplemental food was provided in the form of pelleted Purina® Rat Chow (No. 5012; 22% protein, 4% fat), and alfalfa (Medicago sp.) hay. Each station was provided with 1-2 kg of chow at 3-week intervals from May through September in 1985 and 1986, and at 4-week intervals during the intervening period October 1985 through April 1986. Small bales of alfalfa hay (about 5 kg each) were also placed at each feeding station in May 1985. The supplemental food was covered with a cairn of boulders to prevent disturbance by larger mammals.

I anticipated that bushy-tails would add supplemental food to their foodstores. Thus, food would be available even if the access of bushy-tails to feeding stations was restricted by severe weather, or during reproduction. Bushy-tails were subsequently observed carrying chow to their dens, and I found piles of chow stored in rock crevices on several of the fed areas. Bushy-tails continued to remove chow from the feeding stations throughout the 16 month period of food addition; a total of 1550 kg of chow was provided to the 8 fed areas during this period. There was little use of hay by bushy-tails and hay piles were only replenished if they had become wet and begun to decompose.

2.4. Captive colony

Studies involving the experimental addition of food to natural populations should demonstrate that the food supplied was an appropriate dietary supplement for the species under investigation (Taitt and Krebs 1981; Watson and Moss 1970). Therefore, I determined

whether captive bushy-tails could maintain normal reproduction when restricted to a diet of the supplemental food. Woodrats exhibit high levels of intraspecific aggression when kept in captivity (Egoscue 1962; Kinsey 1976), and when I attempted to maintain a group of 6 bushy-tails in a large (30 x 20 m) enclosure a single male rapidly established dominance and was so aggressive that the death of all other members of the group occurred within 2 days. As an alternative to breeding captive bushy-tails, I live-trapped 7 pregnant females and 6 non-breeding females and housed them in individual cages at the Kananaskis Centre for Environmental Research. Rearing cages measured 1.2 x 0.8 x 0.8 m, with a 0.3 x 0.3 x 0.25 m wooden nestbox in each, and were maintained under conditions of natural photoperiod and temperature. Juveniles were caged separately after weaning in 1.0 x 0.5 x 0.4 m metal cages. Nesting material and known quantities of Purina® Rat Chow and alfalfa (Medicago sp.) hay were provided ad libitum. Two of the breeding females were fed a mixture of Taraxacum sp., Trifolium sp., and Melilotus sp. as a substitute for Medicago sp..

I continued to monitor food consumption and body weight of the 6 non-breeding females at regular intervals during the subsequent winter to investigate seasonal changes in metabolism. Cages remained out of doors during the winter, but were sheltered from wind and precipitation. During periods of sub-zero temperature, the captive bushy-tails were provided with unfrozen water twice a day.

2.5. Statistical analyses

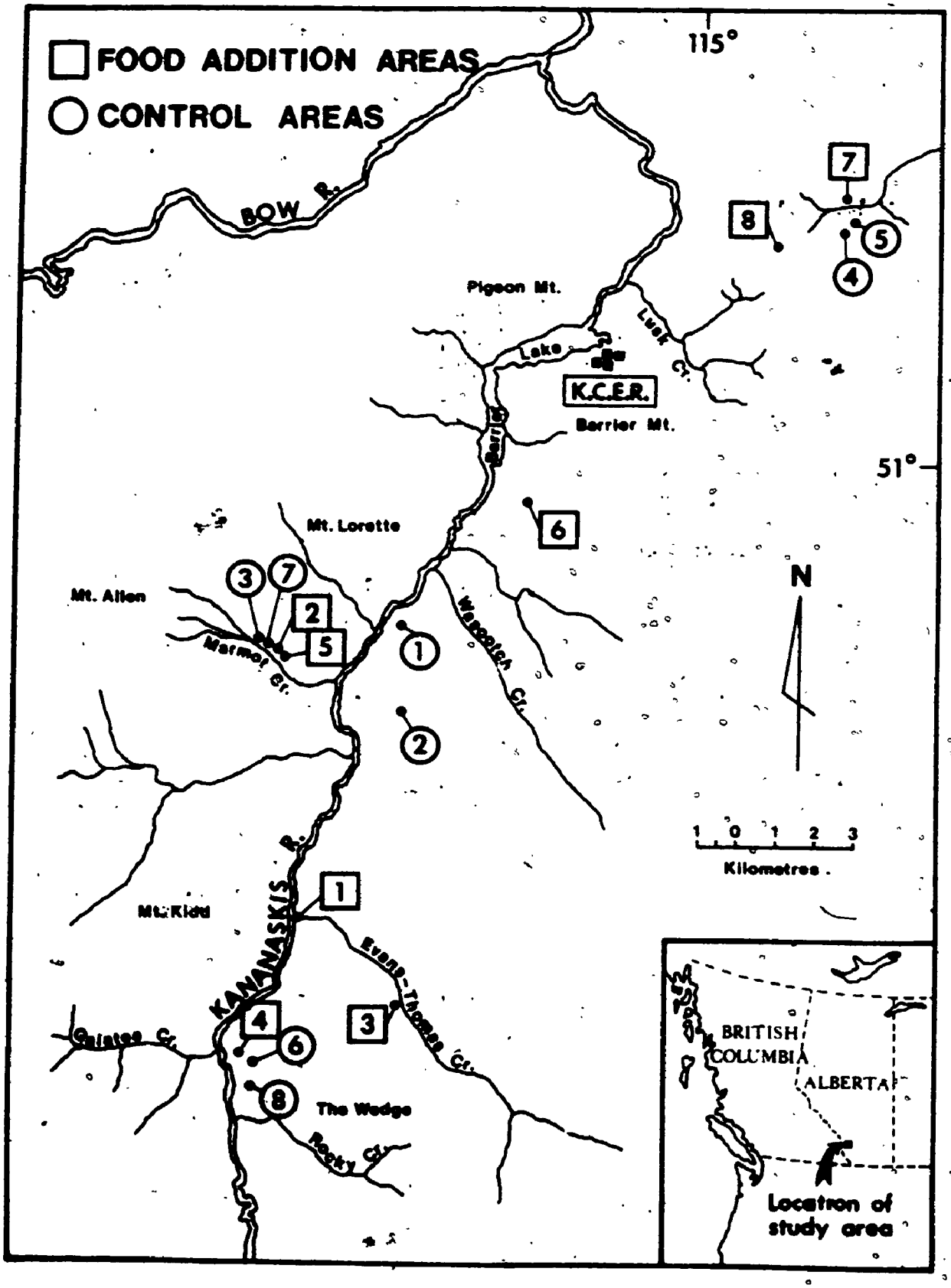
Means are presented ±1 standard error; standard errors are not given for proportions.

Analysis of variance and covariance procedures are referred to as ANOVA and ANCOVA in the text; analyses were performed using the SAS statistical package (PROC ANOVA for balanced designs, PROC GLM for unbalanced designs: SAS Institute 1982). Homogeneity of variance for the data used in these procedures was tested using the F_{max} test (Sokal and Rohlf 1981:403). Log-linear analysis refers to the analysis of multi-way contingency tables using log-linear models (PROC FUNCAT: SAS Institute 1982).

I used 1-tailed tests for comparisons between fed and control areas because I was testing a priori predictions (Chapter 3; Chapter 4) regarding the influence of food addition on reproduction, growth, and group dynamics of bushy-tails. All other comparisons (e.g. between years, sexes, and seasons) were conducted using 2-tailed tests.

FIGURE 1.

Map of the Kananaskis Valley study area, showing the locations of control and fed trapping areas in relation to the Kananaskis Centre for Environmental Research (K.C.E.R.).


FOOD ADDITION AREAS
CONTROL AREAS
115°
51°
BOW R.
Pigeon Mt.
Lake
Lusk Cr.
K.C.E.R.
Barrier Mt.
Barrier L.
Mt. Lorette
Mt. Allen
Marmot Cr.
Wapiabi Cr.
Mt. Kidd
KANANASKIS R.
Evans-Thomas Cr.
Grotto Cr.
The Wedge
Rocky Cr.
N
1 0 1 2 3
Kilometres.
BRITISH COLUMBIA
ALBERTA
Location of study area

CHAPTER THREE - SEASONAL REPRODUCTION AND GROWTH

3.1. Introduction

The study of the social biology of a species should be based on an understanding of the ways in which female behaviour is adapted to meet the demands of the environment. Environmental factors influence the degree to which females aggregate and interact (Rubenstein and Wrangham 1986). Subsequently, the dispersion of females may determine the behaviour patterns which are adaptive for males attempting to maximize their mating success (Emlen and Oring 1977; Erlinge and Sandell 1986).

Seasonal changes in plant production and thermoregulatory demands represent important environmental factors which may constrain the timing of reproduction by small mammals in boreal-montane habitats (Porter and McClure 1984). Unlike a mouse or vole, a mammal the size of a bushy-tail is unlikely to make extensive use of the subnivean environment. Thus, snow-cover may limit access to food. Many herbaceous plants in boreal-montane environments exhibit rapid growth immediately after snow-melt, with above-ground green biomass reaching a maximum in mid-summer (e.g. Kuramoto and Bliss 1970). The nutritional quality of these plants is highest early in the season when plant production is channelled into above-ground production, and declines progressively during the season as production is diverted into reproduction and below-ground storage (Bliss 1985; Bryant et al. 1983; Mooney and Billings 1960). Both above-ground biomass and nutritional quality of the forage will influence the ability of

herbivores to obtain and process plant material at a rate sufficient to meet their nutritional requirements (Sinclair et al. 1982). Thus, food availability is determined by seasonal variation in snow-cover, above-ground plant biomass, and plant nutritional quality.

I investigated the seasonal ecology of bushy-tails in the Kananaskis Valley to determine whether there was evidence that this species was limited by food. Such evidence would support my suggestion that food resources are important in determining bushy-tail social organization. Bushy-tails potentially experience a nutritional shortage during winter, when forage availability is low (Porter and McClure 1984). Thus, bushy-tails should exhibit adaptations to minimize energy requirements during this season. There also exists the potential for bushy-tails to experience a nutritional shortage during reproduction (for breeding females), or during post-weaning growth (for their offspring), because both reproduction and growth are energetically demanding processes (McClure and Randolph 1980; Randolph et al. 1977). I tested the following hypothesis:

Ha: Bushy-tails experience nutritional shortages during winter and during energy-demanding processes such as reproduction and growth.

Studies of other boreal-montane populations of small, herbivorous mammals suggest that a number of general predictions can be made regarding the ecology of species in highly seasonal environments.

Non-hibernating small mammals are unable to rely on metabolic reserves such as body fat to support their energy requirements for extended periods of time (Whittaker and Thomas 1983). Therefore, these

species must continue to forage during winter. Gyug and Millar (1980) proposed, however, that endogenous energy reserves of non-hibernators are important as a short-term buffer against nutritional stress, and that the level of these reserves is intrinsically controlled according to the probability that an individual will experience nutritional stress. If bushy-tails are likely to be nutritionally stressed during winter, they should have larger energy reserves during this season than during summer.

The nutritional demands of small mammals are elevated during lactation (Randolph et al. 1977). Increased nutritional demands might be of little ecological significance if food is superabundant throughout the breeding season. Food availability may, however, vary during the growing season in which case breeding females should time reproduction so that lactation and offspring growth occur during the period of maximum food availability. Furthermore, female bushy-tails may meet part of the increased nutritional demands of reproduction by depleting their endogenous energy reserves (e.g. Sigmodon hispidus: Randolph et al. 1977).

For a generalist herbivore in a boreal-montane environment, food availability is likely highest during the period between rapid spring growth of herbaceous plants (when nutrient content is high) and the mid-summer peak in standing crop (when above-ground green biomass reaches a maximum). Although female bushy-tails may be best able to meet their own nutritional requirements by breeding during this period, other factors may favour females which reproduce earlier in the breeding season: i) bushy-tails may produce several litters each season (Egoscue 1962; Escherich 1981) and early breeding may

allow females to produce more litters than females which initiate breeding later in the season; ii) if overwinter mortality of residents is high, the offspring of early breeders will have the first opportunity to re-occupy vacant habitat; iii) a seasonal decline in nutritional quality of vegetation may result in juveniles born late in the breeding season growing more slowly than those born early in the season (e.g. Slade et al. 1984). Faster growth, and more time available for growth before the onset of winter, would result in early-season juveniles being consistently heavier than the late-season cohort. This would place early-season juveniles at an advantage during competition for critical winter resources. Furthermore, increased body weight may improve the reproductive success of the early-season cohort by allowing them to breed early in the subsequent breeding season.

Although the above factors favour females which attempt to breed early in the season, these females likely face an increased risk of mortality (Fairbairn 1976) and reproductive failure (Smith and Ivins 1983a) since weather conditions and plant growth are unpredictable early in the breeding season (e.g. Morton and Sherman 1978). Females with large endogenous energy reserves may, however, use these reserves to meet the nutritional demands of reproduction during periods of unpredictable food availability (Gyug and Millar 1980). Thus, females with large endogenous reserves may initiate reproduction earlier in the season than do females with smaller reserves (e.g. Smith 1968; Wallage-Drees 1983).

Summary of Predictions:

1) Females increase their energy reserves during winter.
2) Female reproduction is timed so that lactation coincides with the period of maximum food availability.
3) Females use metabolic reserves to help support the energy demands of lactation.
4) Females with large energy reserves breed earlier than those with small reserves.
5) Females which breed early in the season produce more litters than late breeders, and the offspring of these early litters grow more rapidly than offspring born late in the season.

Confirmation of the above predictions would support the hypothesis that bushy-tails experience seasonal food shortages, but would not allow me to determine whether food acts primarily as a proximate, or ultimate, limit to reproduction and growth. However, the hypothesis that food may act as a proximate limit can be experimentally tested by manipulating the abundance of food available to groups of bushy-tails.

Many studies have investigated reproduction of small mammals in seasonal environments, and a number have attempted to experimentally manipulate patterns of reproduction and growth by providing supplemental food. An overview of these latter studies suggests that several predictions can be made regarding the effect of food addition on reproduction and growth of bushy-tails.

Post-weaning growth and adult body weight may be determined in part by food abundance, thus both are likely to increase on fed areas

relative to control areas (e.g. Cole and Batzli 1978; Dobson and Kjelgaard 1985; Sullivan et al. 1983; Taitt 1981; Taitt and Krebs 1983; Wallage-Drees 1983).

Sadleir et al. (1973) and Watts (1970) have suggested that the length of breeding seasons in boreal habitats may be constrained by food abundance. Several studies have demonstrated that populations of small and medium sized mammals provided with supplemental food initiate breeding earlier in the season than those in unmanipulated areas (Boutin 1984; Hansen and Batzli 1978; Taitt 1981; Wallage-Drees 1983; but see Gilbert and Krebs 1981). This suggests that bushy-tails may begin breeding earlier on fed areas than on control areas.

Cameron (1973) and Vaughan and Czaplewski (1985) investigated the influence of litter size on offspring survival in captive woodrats and found that the proportion of young which survived to weaning decreased with increasing litter size. Mortality occurred late in the pre-weaning period, and was apparently related to nutritional stress (N. lepida: Cameron 1973; N. stephensi: Vaughan and Czaplewski 1985). Greater pup mortality during lactation was observed among food-restricted female N. fuscipes than among females fed ad libitum (McClure 1981). Dobson and Kjelgaard (1985) found that female Columbian ground squirrels (Spermophilus columbianus) weaned larger litters on experimentally fed areas than on unmanipulated areas. Thus, female bushy-tails on fed areas should wean more offspring than females on control areas.

Summary of Predictions:

6) Bushy-tails exhibit faster growth and increased overwintered body weight on fed areas than on control areas.

7) Initiation of reproduction occurs earlier in the season on fed areas than on control areas.

8) More juveniles are weaned on fed areas than on control areas.

3.2. Methods

3.2.1. Variation in climate.

Monthly mean values for temperature, sunshine hours, precipitation, and snow-cover were obtained from the climate records of the Kananaskis Centre for Environmental Research (K.C.E.R.; elevation 1400 m) for the period 1984-86. These records were compared to 30-year climate normals for the climate station at K.C.E.R. (Environment Canada 1983) to identify periods of abnormal weather during the period of study.

3.2.2. Seasonal changes in plant biomass and diet quality.

I determined the species composition of freshly stored vegetation in 10 bushy-tail food caches during early fall (Appendix II). A variety of plant species were stored in substantial quantities, which confirmed that bushy-tails are generalist herbivores in the Kananaskis Valley (see also Salt and Clarke 1979). Therefore, I used total above-ground biomass of green vegetation (Milner and Hughes 1968) as an index of seasonal forage abundance. Vegetation was sampled on circular 1 m^2 quadrats located on unforested slopes adjacent to 5

trapping areas (Appendix I). Quadrats were located in a 20 x 20 m cruciform pattern, centered on a point selected randomly from an aerial photograph of each area. Vegetation was clipped 5 mm above ground level from a different quadrat in each area at approximately 3-week intervals between March and September 1986. Green vegetation was sorted from the sample, dried to constant weight at 55°C, and weighed to the nearest 1.0 g.

I defined the period of maximum forage availability as the interval between the date of maximum production of green biomass (P_{max}) and the date of maximum standing crop (SC_{max}). This interval should correspond to the period of high plant nutrient content and maximum above-ground biomass (Bliss 1985, Mooney and Billings 1960). I quantified the seasonal trend in plant biomass by fitting a 3rd-order polynomial equation to the raw data using curvilinear regression (Hunt 1982). P_{max} and SC_{max} were estimated by setting the first and second derivatives of the polynomial to zero.

It is difficult to estimate diet digestibility directly for small herbivores because of the difficulty in obtaining forage samples that are representative of the plant material selected by the animals. Servello et al. (1983) analyzed stomach contents of voles (Microtus pinetorum) and reported that the fraction of stomach contents that was soluble in neutral detergent solution (i.e. cell solubles: Van Soest 1967) was highly correlated with the dry matter digestibility of the voles' diet. Therefore, I estimated diet digestibility by measuring the neutral detergent solubility of bushy-tail stomach contents using a procedure modified from Goering and Van Soest (1970) and Servello et al. (1983). Stomach contents were dried for 48 h at 55°C, and weighed

to the nearest 0.01 g. Servello et al. (1983) noted that estimates of cell solubles for individuals which had only small amounts of forage in their stomachs tended to underestimate the true digestibility of their diet. For this reason, I excluded stomach contents weighing less than 0.5 g dry weight from further analysis. Dried contents were ground using a Wiley® Mill with a 40-mesh screen, and a subsample of approximately 0.2 g (weighed to the nearest 0.0005 g) was refluxed in 10 ml of neutral detergent solution for 1.5 h in 100-ml Goldfisch® beakers. The residue was filtered under suction using preweighed No. 5 porosity filter paper, washed with hot water followed by acetone, dried to constant weight at 55°C. The final residue (fibre insoluble in neutral detergent) was weighed to the nearest 0.0005 g. Cell solubles ($g \cdot 100g^{-1}$) were calculated as 100 minus the percent detergent-insoluble residue.

Seasonal changes in diet digestibility were examined by comparing data from summer (15 June through 15 September) and winter (15 November through 15 February) samples using t-tests. The raw data were $\log_e$-transformed to standardize the variances.

3.2.3. Influence of season and reproduction on food consumption.

I used the weight of stomach contents from kill-trapped bushy-tails as an index of forage abundance on their feeding range during summer and winter. Weight of stomach contents has been shown to be highly correlated with the amount of food consumed by small herbivores over a 4-6 h period prior to time of measurement (Collins and Smith 1976; Gentry et al. 1975). Since kill-trap spacing was held constant among seasons, the average area traversed by a foraging

bushy-tail before encountering a trap was likely similar among seasons (e.g. Hansson 1971). Thus, seasonal changes in weight of stomach contents should correspond to changes in the abundance of forage encountered before the point of capture on the feeding range. Note that this interpretation of weight of stomach contents differs from that of Golley (1967), who suggested that mean weight of stomach contents was a measure of food consumption halfway though a foraging bout.

I monitored seasonal changes in daily food consumption and body weight of 6 captive non-breeding females at 20-day intervals during summer (15 June through 15 September) and the subsequent winter (15 November through 15 February). As this sampling method resulted in repeated measures for each individual, I compared food consumption during winter and summer using a two-way ANOVA with individual and season as factors. A paired t-test was used to compare body weight changes of breeding females between parturition and weaning with weight changes of non-breeding females over the equivalent period of time.

Schierwater and Klingel (1986) have demonstrated that laboratory estimates of the energetic cost of reproduction for small mammals are representative of their energetic costs under natural conditions. I monitored 7 breeding females at 2-day intervals during the course of gestation and lactation to determine the influence of reproduction on daily food consumption and body weight. I calculated a mean daily consumption for each breeding female during the last 2 weeks of gestation, during the first 2 weeks of lactation, and during the first 2 weeks after weaning, and compared these data with equivalent

estimates for 6 non-breeding females using t-tests.

Food consumption was estimated by providing known quantities of food (nearest 0.1 g wet weight) to captive bushytails at 2-day intervals during the breeding season, and at 20-day intervals for the remainder of the year. The dry weight of this food was estimated by drying subsamples to constant weight at 55°C. Daily consumption was calculated from the dry weight of food remaining uneaten at the end of each interval. Total energy assimilation was calculated by comparing food consumption and faecal production. Energy contents of food and faeces were estimated by bomb calorimetry. Digestive efficiency was calculated from the energy loss in faeces, measured separately for winter/non-breeding, summer/non-breeding, and summer/lactating females (n=6 for each group). Assimilation efficiency was estimated as digestive efficiency minus 2% urinary loss (Grodzinski and Wunder 1975).

The attainment of independence from the mother is a gradual process for young mammals, involving physiological, nutritional and behavioural components (Millar et al. 1986). I estimated onset of nutritional independence as the date at which nestlings began to consume solid food (evidenced by the production of dark faeces; Egoscue 1962). I also estimated the proportion of solid food consumed by 1 litter of nestlings by recording nestling faecal production at 2-day intervals during lactation. In calculating this estimate, I assumed that the assimilation efficiency of nestlings was similar to that of the mother.

3.2.4. Influence of season and reproduction on body composition.

The influence of season and reproductive status on body composition was determined by necropsy and ether extraction of kill-trapped adult female bushy-tails. Carcasses (excluding stomach contents, skull, reproductive tract, embryos, and pelt) were ground in a meat-grinder and dried for 72 h at 75 °C. Carcass dry weight was recorded (nearest 0.1 g) and the carcass was more finely ground in a Moulinex® type 228-102 coffee grinder. Two 4 g subsamples were dried for a further 24 h, weighed (nearest 0.001 g), and placed in pre-weighed Whatman® 22x80 cellulose extraction thimbles. These samples were extracted in petroleum ether for 6-8 h using a Soxhlet® extraction apparatus, dried, and reweighed. Fat content of the pelt was determined by soaking the intact pelt in ether for 24 h. Total fat content (FAT) was calculated as the mean of the two replicate estimates of carcass fat, plus pelt fat. Fat-free dry weight (FFDW) was calculated as carcass dry weight minus carcass fat. Energy content (ENERGY) was estimated from the equation: ENERGY (kJ) = 19.2FFDW + 38.1FAT (after Kaufman and Kaufman 1975; 1 kJ = 4.1868 kcal)

FAT, FFDW, and ENERGY were corrected for variation in skeletal size using ANCOVA. Corrected FAT values were calculated as the mean value for FAT plus residual values from the linear regression of FAT on HEAD LENGTH cubed. Values for FFDW and ENERGY were corrected in a similar manner. T-tests on $\log_e$-transformed data were used for planned comparisons of body composition between non-breeding females in winter and summer, and between females in late pregnancy and lactation.

Whittaker and Thomas (1983) estimated the period of nutritional support available to showshoe hares (Lepus americanus) from their

endogenous reserves by assuming that 100% of their fat reserves and 30% of their protein reserves were available for catabolism during nutritional stress. The ash content of bushy-tail FFDW was 13.6% (± 0.4%; n=6). Therefore, I assumed that bushy-tails could catabolize 100% of FAT and 25% of FFDW during nutritional stress, and that there was negligible loss of energy during this conversion. The number of days of potential support available from endogenous reserves was calculated by dividing the energy equivalent of these reserves by the corresponding estimates of daily energy assimilation (from 3.3.3).

3.2.5. Post-weaning growth and adult body weight.

Ebert (1980) presented a method for calculating growth curves from mark-recapture data (i.e. where individuals are of unknown age, but increments in body weight between each recapture have been recorded). As there was unavoidable variation in the interval between recaptures of juvenile bushy-tails, I excluded data from recaptures separated by less than 20 days or more than 25 days from further analysis. I then standardized the remaining weight increments to an interval of 21 days by assuming linear change in weight over each interval. This assumption caused negligible bias in the subsequent calculations. I then regressed weight at recapture (T+21 days) against weight at previous capture (T days). These data were transformed to test the fit of the data to monomolecular (i.e. non-inflected), Gompertz, and logistic growth models using the 'minimum sums of squares of error' method (Ebert 1980). Although Zullinger *et al.* (1984) suggested that the Gompertz equation provides a good approximation of mammalian growth patterns, I found that a

monomolecular curve provided the best fit to post-weaning growth data for bushy-tails because inflection of the growth rate occurred shortly after weaning (see Egoscue 1962; Martin 1973).

Monomolecular equations were calculated from the regression of Weight (T+21) on Weight (T). As both Weight (T) and Weight (T+21) are measured with error (i.e. Model II data), I followed the suggestion of Sokal and Rohlf (1981:550) that reduced major axis (RMA) regression be used to estimate the intercept and slope parameters of the regression equation (B' and B", respectively), but that Ordinary Least Squares (OLS) estimates of variance may be used to compare regression slopes and intercepts. The appropriate monomolecular equation was calculated as follows (after Ebert 1980):

$$\text{Weight}(t) = K(1-e^{-bt}) \qquad \text{(Eqn.1)}$$

where: $b = -\log_e B''$

$K = B'/(1-B'')$

Monomolecular equations were calculated separately for sexes, and for fed and control areas. Calculation of growth curves for free-ranging bushy-tails required an estimate of the age and weight at which juveniles began to enter the trappable population. As the sex ratio of the total sample of live-trapped juveniles did not differ from unity (125 male: 123 female), I assumed that mean weight of the lightest 10 males and 10 females captured in live-traps was representative of offspring weight at behavioural independence. Based on pre-weaning growth of the 7 captive litters described in 2.4., both of these weights (103 g and 92 g for males and females respectively)

corresponded to 23 days of age. Birth dates and weaning dates (date of birth plus 23 days) were estimated by back-calculation from the monomolecular equation using the following equation:

$$\text{DAYS OF AGE} = \frac{I}{b_i} \times \log_e \frac{1 - (w / K_i)}{1 - (W' / K_i)} + 23 \qquad \text{(Eqn.2)}$$

where: K_i = K parameter for cohort i (from Eqn.1)
b_i = b parameter for cohort i (from Eqn.1)
I = trapping interval (i.e. 21 days)
w = estimated body weight (g) at weaning
W' = body weight (g) at first capture

To test for seasonal variation in growth rate, juveniles were separated into "spring" and "summer" cohorts on the basis of those with estimated weaning dates before and after 1 July. ANCOVA was used to determine whether sex, food addition, or season had any effect on post-weaning growth. As this analysis demonstrated that all 3 factors had a significant influence on growth rate (see 3.3.5), I re-estimated weaning dates from equations calculated separately for season, as well as sex and food addition, and revised the seasonal cohorts before conducting the final ANCOVA.

To increase sample size, I included growth data obtained from live-trapping in areas other than the 16 fed and control areas. These data were pooled with data from control areas.

To determine whether post-weaning growth during the season of birth influenced body weight during the subsequent breeding season, I correlated weight of juveniles live-trapped during early fall (September through October 1985) with their weight when recaptured as

pre-reproductive yearlings in the subsequent spring (15 April through 15 May 1986).

Energy reserves could not be directly estimated for adult bushy-tails on the control and fed areas. Gross body weight (GBW), and gross weight corrected for skeletal size (CBW) were used as indirect measures of body reserves. Gross weight was corrected for skeletal size using ANCOVA, using the method described in 3.2.4. Data for control and fed areas were compared using a two-way ANOVA with sex and area as factors.

3.2.6. Initiation of reproduction.

Date of first parturition was used as a measure of the onset of breeding. As pregnant bushy-tails could not be directly monitored in their dens, I used two indirect techniques to estimate their date of parturition. First, palpation of captive bushy-tails during pregnancy indicated that females classified as "advanced pregnancy" were in the last week of gestation. Mean dates of parturition for these females were estimated as date of capture plus 3 days. Second, some breeding females could be unambiguously associated with juveniles captured shortly after weaning. I estimated parturition date for these females by backdating from the weight of their juveniles at first capture, as described in 3.2.5.

Several species of small mammal exhibit a pattern of body weight variation during winter such that small individuals exhibit positive growth whereas large individuals lose weight (Iverson and Turner 1974; Slade et al. 1984). Since body weight may not be an accurate predictor of age for overwintered bushy-tails, I divided bushy-tails into

juvenile, yearling, and adult age-classes on the basis of head length and pelage. ("Overwintered" is used as an inclusive term for both yearlings and adults). Juveniles maintained a characteristic grey pelage during their first summer, and most yearlings present during 1985 and 1986 were initially captured as juveniles during the previous season. Any untagged overwintered bushy-tail with a head length less than 53 mm (for females) or 55 mm (for males) that appeared on a trapping area was classified as a yearling. Any untagged overwintered bushy-tail with a head length greater than the above values was considered of unknown age.

Date of first parturition was regressed against body weight of females captured in pre-breeding condition (i.e. non-perforate) on control areas during the period 15 April through 15 May in 1985 and 1986. ANCOVA was used to determine the influence of body weight, year, and age on date of first parturition. I also estimated between-year variation in the onset of breeding from the date of first parturition on each area. Mean dates of onset on control and fed areas in 1985 and 1986 were compared using t-tests.

To further investigate the timing of female reproduction, I compared the distribution of weaning dates for juveniles captured during 1986 (see 3.2.5) with the period of maximum food availability (as defined in 3.2.2).

3.2.7. Number of litters and litter size.

The number of litters for each live-trapped female was estimated by palpation (for pregnancy) and examination of the nipples (for lactation). Pregnancies which were not associated with subsequent

lactation were classified as failed breeding attempts. Some reproductive females disappeared from trapping areas during the breeding season. Consequently, estimates of litters per female were calculated only for those females which remained on an area for the duration of the breeding season. The influence of year and food addition on the number of litters per female was assessed using log-linear analysis.

Direct estimates of litter size were obtained from the number of visible embryos recorded during necropsy of kill-trapped females and from litter size at birth for captive females. In the field, it was not possible to gain access to nestlings before weaning. Thus, I was unable to assess the maternity of juveniles captured on areas where more than one female bred. I estimated mean litter size at weaning by dividing the total number of juveniles captured on each area (excluding probable immigrants, see 4.2.3) by the number of litters produced on each area. Mean production of juveniles per resident female was calculated in an equivalent manner.

The influence of year and food addition on litter size at weaning, and juveniles per female, was tested using a two-way ANOVA. Spearman rank correlation was used to test for a relationship between litter size at weaning and the number of adult females on each area.

3.3. Results

3.3.1. Variation in climate.

There was marked seasonal variation in temperature and snow-cover in the Kananaskis Valley (Figure 2). Comparisons between years

indicated that the winter of 1984/85 had a relatively consistent level of snow-cover from September 1984 through April 1985. In contrast, temperatures were unusually mild during January and March of 1986, and there was a marked reduction of snow-cover during these months.

3.3.2. Seasonal changes in plant biomass and diet quality.

There was negligible primary production on the vegetation quadrats during winter. Measurable production began during April 1986, maximum production of green biomass occurred about 5 June, and maximum standing crop was reached about 1 August (Figure 3). Increased primary production was associated with increased temperature and increased hours of sunshine during summer (Figure 3).

The digestibility of forage, as estimated by neutral detergent analysis of the stomach contents, was lower in winter than in summer (Table 1a). Digestibility of stomach contents did not vary between the sexes ($t=0.2$, $p=0.9$) or between breeding and non-breeding females ($t=1.5$, $p=0.14$).

3.3.3. Influence of season and reproduction on food consumption.

Weight of stomach contents was lower in winter than in summer for both sexes (Table 1a). Weight of stomach contents was not influenced by female reproductive status (non-breeding females compared with pregnant or lactating females; $t=0.76$, $p=0.5$).

Total daily food consumption by captive non-breeding females was 18% lower in winter than in summer, and relative food consumption ($g \cdot Kg^{-1} \cdot day^{-1}$) was 12% lower in winter than in summer (Table 1b). There was no indication that bushy-tails underwent torpor to reduce

energy requirements during winter. Captive bushy-tails were active throughout the year, and tracks in the snow around dens indicated that free-ranging bushy-tails were also active during winter.

There was no mortality of nestlings in the captive colony (n=7 litters), which demonstrated that the supplemental food was of sufficient quality to support the nutritional requirements of reproduction.

Captive bushy-tails provided with Purina® Rat Chow and alfalfa hay ad libitum exhibited a marked preference for the chow, which comprised 76% of their daily intake on a dry weight basis. Total daily food consumption by captive females during the last 2 weeks of gestation was 24% higher than the equivalent daily consumption by non-breeding females (Figure 4, $t=3.3$, $p<0.01$). Consumption values for breeding females during the first 2 weeks of lactation were 93% higher than for non-breeding females ($t=10.3$, $p<0.0001$), whereas consumption by post-weaning females and non-breeding females did not differ significantly ($t=0.7$, $p=0.5$).

The onset of nutritional independence of nestlings occurred about 15 days after birth (range 14-18 days; n=7 litters). Changes in faecal production for 1 litter monitored throughout lactation indicated that consumption of solid food by these nestlings increased markedly when their eyes opened on day 15 (Table 2). Nestling faecal production amounted to 28% of total faecal output by the mother and litter during the third week of lactation, although this value was unreplicated and should be interpreted with caution.

3.3.4. Influence of season and reproduction on body composition.

Captive bushy-tails had lower gross body weight in winter than in summer (Table 1b) despite the availability of ad libitum food during both seasons. Winter weight loss was initiated in early fall; with captive adults losing a mean of 5 g (±5 g; n=6) per month during October. Free-ranging adults lost a mean of 6 g (±4 g; n=40) over the same period. Free-ranging overwintered females had more fat in winter than summer (Table 3a. $t=3.2$, $p<0.005$). In contrast, fat-free dry weight tended to be lower in winter than in summer, although the difference was not significant ($t=1.2$, $p=0.2$).

During lactation, breeding females (n=7) lost a mean of 26 g body weight relative to non-breeding females over the same period (n=6; paired t-test; $t=3.8$, $p<0.005$). Free-ranging females in late pregnancy were fatter ($t=5.5$, $p<0.0001$) and had a higher energy content ($t=3.7$; $p<0.005$) than lactating females (Table 3b), although these groups did not differ in fat-free dry weight ($t=1.0$, $p=0.3$).

The energy content of the diet was estimated as 18 kJ·gDW. Digestive efficiency was estimated as 73% (± 2%; n=18). This value did not vary among winter/non-breeding, summer/non-breeding, and summer/lactating groups (one-way ANOVA; $F=0.19$, $p=0.8$). The period of potential nutritional support available to overwintered females from their endogenous reserves was about 3 days during winter and less than 1 day during lactation (Table 4).

3.3.5. Post-weaning growth and adult body weight.

Growth curves for weaned bushy-tails are given in Figure 5; parameters for the corresponding equations are given in Appendix IV.

Results from the ANCOVA on the mark-recapture growth data indicated that the SEX, FOOD, YEAR, and SEASON main effects, and the WEIGHT(T)*YEAR interaction, were non-significant ($p < 0.2$). Non-significant main effects indicated that the y-intercept of the regression (B' in Eqn.1) was not influenced by these factors. (B' corresponds approximately with body weight at weaning).

When the above variables were removed from the model, a subsequent reduced-model ANCOVA indicated that all remaining WEIGHT(T)*(CLASS VARIABLE) interactions were highly significant, and that a significant WEIGHT(T)*SEX*SEASON interaction was present (Table 5). Significant WEIGHT(T)*(CLASS VARIABLE) interactions indicate that the slope of the linear regression (B" in Eqn.1), and therefore growth rate, was significantly higher for males, food addition areas, and the spring cohort than for females, control areas, and the summer cohort. Differential growth of males and females was less pronounced in the summer cohort than in the spring cohort (see Appendix IV), which resulted in a significant WEIGHT(T)*SEX*SEASON interaction.

A number of juveniles survived the winter of 1985/86 and were recaptured during the subsequent spring. Spring body weight of these pre-reproductive yearlings was highly correlated with their body weight during the preceeding fall ($r=0.71$, $n=27$, $p<0.001$). Yearlings were heavier on fed areas than on control areas in spring ($t=3.23$, $p<0.005$).

Gross body weight, head length, and body weight corrected for skeletal size of overwintered adults were similar on fed and control areas before the addition of food (Table 6a). By the end of the experiment, overwintered bushy-tails on fed areas were heavier and

structurally larger than adults on control areas, although size-corrected weight did not vary significantly between areas (Table 6b).

Body weight of overwintered females on the kill-trapping areas was positively correlated with their total carcass fat ($r=0.50$, $n=48$, $p<0.001$).

3.3.6. Initiation of reproduction.

Yearling female bushy-tails were lighter than adults (Table 7. $t=5.11$, $p<0.0001$), and bred later in the season than did adults ($t=2.27$, $p<0.05$). However, yearlings and adults did not differ in the number of litters produced per season (Fisher exact test, $p=0.51$).

Results from the ANCOVA indicated that there was a negative relationship between female body weight and onset of breeding ($F=9.12$, $p<0.01$) and that there was a significant difference in onset of breeding between 1985 and 1986 that was not related to differences in weight between years (9.2 days earlier in 1986; $F=7.89$, $p<0.02$). The relationship between body weight and onset of breeding, with this year effect removed, is shown in Figure 6.

There was no difference between yearlings and adults in the onset of breeding once the effect of differences in weight had been removed (ANCOVA; $F=0.17$, $p=0.7$). Furthermore, the negative relationship between weight and onset of breeding remained significant when yearlings and adults were analyzed separately ($F=5.7$, $p<0.05$; $F=8.9$, $p<0.05$; respectively).

The mean date of onset of breeding did not differ between fed and control areas in 1985 (6 June and 7 June, respectively; $t=0.22$, $p=0.8$).

but was earlier on the fed areas than on the control areas in 1986 (4 May and 29 May, respectively; $t=2.84$, $p<0.02$). The majority of juveniles were weaned during the period of maximum food availability on control and fed areas (Figure 7). However, the proportion of juveniles weaned prior to this period was higher on fed areas (31%) than on control areas (10%; Fisher exact test, $p<0.05$).

3.3.7. Number of litters and litter size.

All overwintered females kill-trapped from June through August (n=46) exhibited evidence of reproduction (i.e. embryos or recent placental scars). Only 1 of the 37 overwintered females on the live-trapping areas in 1985 did not breed, and all overwintered females on these areas bred in 1986 (Appendix III). No female had more than 2 litters during one breeding season. Females which were successful in producing 2 litters began breeding an average of 13 days earlier than females which produced only 1 litter ($t=2.88$, $p<0.005$). The proportion of females which had 2 litters increased significantly between 1985 and 1986. Furthermore, the proportion of females having 2 litters was higher on fed areas than control areas (Table 8).

The modal litter size based on embryo counts was 3 (range 3-5). Litter size at birth in captivity did not differ significantly from embryo counts during gestation (Table 9. $t=0.4$, $p=0.7$). Females with a litter size of 3 tended to be smaller than females with larger litters (based on head length; $t=1.7$, $p=0.10$). The relationship between body weight and litter size could not be determined because females were kill-trapped at different stages of gestation and body reserves were known to vary during reproduction (see 3.3.3).

Estimates for mean litter size at weaning ranged from 2.0 on control areas in 1985 to 2.9 on fed areas in 1986. Litter size was significantly higher on fed areas than control areas, but did not vary significantly between years (Table 10).

The mean production of weaned juveniles per resident female was significantly higher in 1986 than in 1985, and significantly more juveniles were weaned on fed areas than control areas (Table 11). The mean production of weaned juveniles per female tended to be negatively correlated with the number of breeding females on each area. This negative trend was more pronounced on control areas (1985 and 1986 treated as independent samples; $r_s = -0.43$, $n=16$, $p=0.09$) than on fed areas ($r_s = -0.32$, $n=16$, $p=0.23$).

Table 1. Seasonal changes in a) digestibility and mass of stomach contents of kill-trapped overwintered bushy-tails, and b) food consumption and body weight of 6 non-breeding overwintered females fed ad libitum in captivity. Seasons were defined as summer (15 June through 15 September), and winter (15 November through 15 February). Log-transformed variances were homogeneous (F_{max} test; $p>0.05$). Means presented ± 1 standard error; sample sizes in parentheses.

	WINTER	SUMMER		
a) Stomach contents				t-test
DIGESTIBILITY: ($g \cdot 100gDW^{-1}$)	59.9 ± 1.3 (15)	70.7 ± 0.8 (57)	t=6.16	p<0.0001
MASS (gDW):				
Male	1.6 ± 0.3 (25)	4.5 ± 0.9 (12)	t=2.64	p<0.05
Female	1.2 ± 0.1 (7)	2.3 ± 0.3 (31)	t=2.14	p<0.05
b) Food consumption				Repeated measures ANOVA
GROSS CONSUMPTION: ($gDW \cdot day^{-1}$)	14.3 ± 0.4 (24)	11.5 ± 0.6 (24)	F=29.1	p<0.0001
BODY WEIGHT (g):	282 ± 9 (24)	305 ± 7 (24)	F=22.4	p<0.0001
RELATIVE CONSUMP.: ($gDW \cdot Kg^{-1} \cdot day^{-1}$)	51 ± 2 (24)	58 ± 2 (24)	F=6.5	p<0.02

Table 2. Development of nutritional independence by 1 litter of juvenile bushy-tails. The production of dark faeces was used as an index of the amount of solid food being consumed by the mother and her offspring (n=5); faeces from the nestlings and the mother were readily distinguished on the basis of size.

Days since birth	Mass of dark faeces ($g.day^{-1}$)		
	MOTHER	NESTLINGS	TOTAL
9-10	9.30	0.00	9.30
11-12	8.25	0.00	8.25
13-14	10.75	0.05	10.80
15-16.....eyes open.....	10.25	0.90	11.15
17-18	7.50	4.15	11.75
19-20	5.00	8.20	13.20
21-22.....nestlings weaned from mother[a]			
23-25	3.95	14.05	N/A
26-27	4.00	18.50	N/A

a. Behavioural independence from mother assessed as date of emergence from nest box (22 days of age).

Table 3. Influence of a) season, and b) reproductive status on body composition of overwintered female bushy-tails. Seasons defined as summer (15 June through 15 September), and winter (15 November through 15 February). Carcass fat content (FAT), fat-free dry weight (FFDW) and energy content (ENERGY) were corrected for variation in skeletal size using ANCOVA. Log-transformed variances were homogeneous (F_{max} test, $p>0.05$). Means presented ± 1 standard error.

	n	FAT (g)	FFDW (g)	ENERGY (kJ)[a]
a) SEASON:				
Winter/non-breeding	17	9.3 ± 1.1	45.3 ± 1.4	1226 ± 60
Summer/non-breeding	11	5.2 ± 1.1	47.5 ± 1.1	1111 ± 52
b) REPRODUCTIVE STATUS:				
Pre-breeding[b]	17	6.2 ± 0.7	43.5 ± 1.0	1074 ± 36
Early pregnancy	6	8.1 ± 1.1	43.0 ± 2.6	1137 ± 40
Advanced pregnancy	6	8.9 ± 1.6	47.4 ± 1.0	1252 ± 67
Lactating	11	3.0 ± 0.3	45.4 ± 1.5	986 ± 39
Pregnant and lactating	3	4.4 ± 1.3	47.7 ± 2.5	1086 ± 90
Post-breeding[b]	11	5.7 ± 1.0	48.3 ± 1.3	1146 ± 54

a. Calculated as ENERGY = 19.2FFDW + 38.1FAT (after Kaufman and Kaufman 1975).

b. Excluding winter data.

Table 4. Summary of seasonal energetics for overwintered female bushy-tails. The period of potential metabolic support was calculated by comparing daily energy assimilation with estimates of the endogenous energy reserve.

	Food consumption[a] ($g \cdot day^{-1}$)	Assimilated energy[b] ($kJ \cdot day^{-1}$)	Endogenous reserves[c] (kJ)	Potential support (days)
WINTER:				
Non-breeding	14.7	188	572	3.0
SUMMER:				
Non-breeding	16.4	210	426	2.0
Lactating	31.1	397	332	0.8

a. For captive bushy-tails.

b. Assuming energy equivalent of the diet to be 18 $kJ \cdot gDW^{-1}$ (this study), 73% digestive efficiency (this study), and 2% urinary loss (Grodzinski and Wunder 1975).

c. For free-ranging bushy-tails, assuming 100% catabolism of fat and 25% catabolism of fat-free dry weight (after Whittaker and Thomas 1983).

Table 5. Analysis of covariance table for the influence of sex, food addition, and season on post-weaning growth of bushy-tails. Juveniles weaned before July 1 were classified as spring-cohort; those weaned later were classified as summer-cohort. Main effects (SEX, FOOD, SEASON) were non-significant ($p>0.2$), and were removed from the model. The reduced-model R^2 was 0.90.

Source of Variation in WEIGHT(T+21days):	df	SS	F
WEIGHT(T)	1	511129	1387.1 ***
WEIGHT(T)*SEX	1	36986	100.4 ***
WEIGHT(T)*FOOD	1	21524	58.4 ***
WEIGHT(T)*SEASON	1	14687	39.9 ***
WEIGHT(T)*SEX*SEASON	1	4430	12.0 **
WEIGHT(T)*FOOD*SEASON	1	631	2.3 ns
WEIGHT(T)*SEX*FOOD	1	463	1.7 ns
ERROR	171	62276	
TOTAL	178	652126	

(*** indicates $p<0.0001$)

(** indicates $p<0.001$)

Table 6. Comparison of gross body weight (GBW), head length (HEAD), and body weight corrected for variation in skeletal size (CBW) of overwintered bushy-tails on control and experimental areas, a) before the addition of food (August 1984), and b) after the addition of food (August 1986). Body weight was corrected for variation in skeletal size using ANCOVA (see text for details). Control and experimental areas were compared using two-way ANOVA with sex and area as factors. The reported F-values refer to the component of variance explained by area. Variances were homogeneous (F_{max} test, $p>0.05$) and two-way interactions were non-significant. Means presented ±1 standard error.

a) BEFORE FOOD ADDITION:

	CONTROL AREAS		EXPERIMENTAL AREAS			
	Male (n=5)	Female (n=14)	Male (n=5)	Female (n=12)	Between-area comparison	
GBW (g)	428 ± 14	313 ± 9	416 ± 15	308 ± 9	F=0.4	p=0.5
HEAD (mm)	60.2±1.0	56.7±0.3	59.0±0.8	57.3±0.4	F=0.2	p=0.9
CBW (g)	417 ± 11	307 ± 8	417 ± 14	295 ± 7	F=0.9	p=0.3

b) AFTER FOOD ADDITION:

	CONTROL AREAS		EXPERIMENTAL AREAS			
	Male (n=7)	Female (n=17)	Male (n=12)	Female (n=16)	Between-area comparison	
GBW (g)	413 ± 12	294 ± 8	440 ± 12	323 ± 9	F=7.8	p<0.005
HEAD (mm)	58.0±0.5	55.0±0.4	59.5±0.5	56.2±0.4	F=8.3	p<0.005
CBW (g)	424 ± 9	308 ± 7	437 ± 11	322 ± 6	F=2.8	p=0.1

Table 7. Body weight, date of first parturition, and proportion with 2 litters for yearling and adult female bushy-tails on control areas in 1985 and 1986. Means presented ± 1 standard error; sample sizes are given in parentheses.

	Yearling	Adult
Pre-breeding body weight (g)	239 ± 7 (14)	297 ± 9 (9)
First parturition (Julian date)	155 ± 4 (14)	144 ± 3 (9)
Proportion with 2 litters	42% (19)	59% (17)

Table 8. Influence of year and food addition on the proportion of females producing 2 litters. Breeding females which disappeared from trapping areas during the breeding season (n=15) were excluded from this analysis. The two-way interaction was non-significant; sample sizes are given in parentheses.

	1985	1986	LOG-LINEAR ANALYSIS			
			Source	df	X^2	
CONTROL AREAS	30% (17)	62% (19)				
			Year	1	8.41	$p<0.005$
FED AREAS	45% (14)	85% (14)	Food	1	4.51	$p<0.05$

Table 9. Embryo counts for kill-trapped females, and litter size at birth for captive bushy-tails.

	Litter size				
	3	4	5	Mean ± SE	(n)
Embryos	11	7	0	3.39 ± 0.12	(18)
Neonates	5	2	1	3.50 ± 0.27	(8)

Table 10. Influence of year and food addition on the mean number of juveniles weaned per litter on each trapping area. The mean number of juveniles weaned per litter was estimated by dividing the total number of juveniles weaned on an area by the number of litters produced on that area. Variances were homogeneous (F_{max} test; $p>0.05$) and the two-way interaction was non-significant. Means presented ± 1 standard error; the number of areas is given in parentheses.

Area	1985	1986	TWO-WAY ANOVA		
			Source	$F_{(1,29)}$	
CONTROL	1.98 ± 0.30 (8)	2.09 ± 0.39 (8)			
			Year	0.54	ns
FED	2.50 ± 0.47 (8)	2.89 ± 0.32 (8)	Food	3.22	$p<0.05$

Table 11. Influence of year and food addition on the mean number of juveniles per breeding female on each trapping area. Breeding females which disappeared from trapping areas during the breeding season were included in this analysis. Variances were homogeneous (F_{max} test; $p > 0.05$) and the two-way interaction was non-significant. Means presented ± 1 standard error; the number of areas is given in parentheses.

Area	1985	1986	TWO-WAY ANOVA		
			Source	$F_{(1,29)}$	
CONTROL	2.52 ± 0.45 (8)	3.46 ± 0.73 (8)			
			Year	4.83	$p<0.05$
FED	3.50 ± 0.68 (8)	5.32 ± 0.65 (8)	Food	5.07	$p<0.02$

FIGURE 2.

Seasonal changes in temperature and snow depth at the Kananaskis Centre for Environmental Research from 1984 through 1986. The histograms indicate mean values (by month) for each year and the dotted line indicates temperature normals for the period 1951-1980 (Environment Canada 1983).

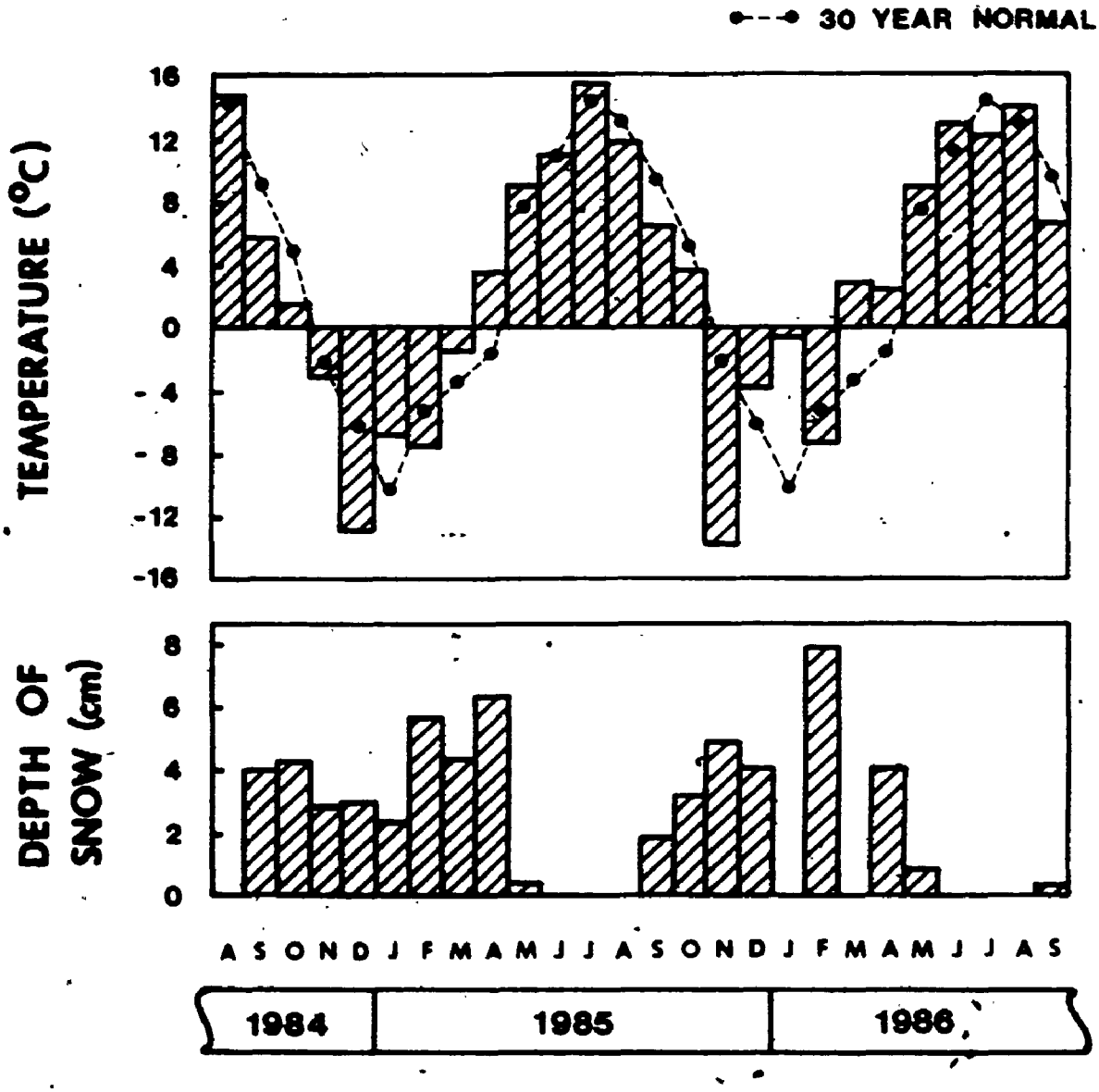
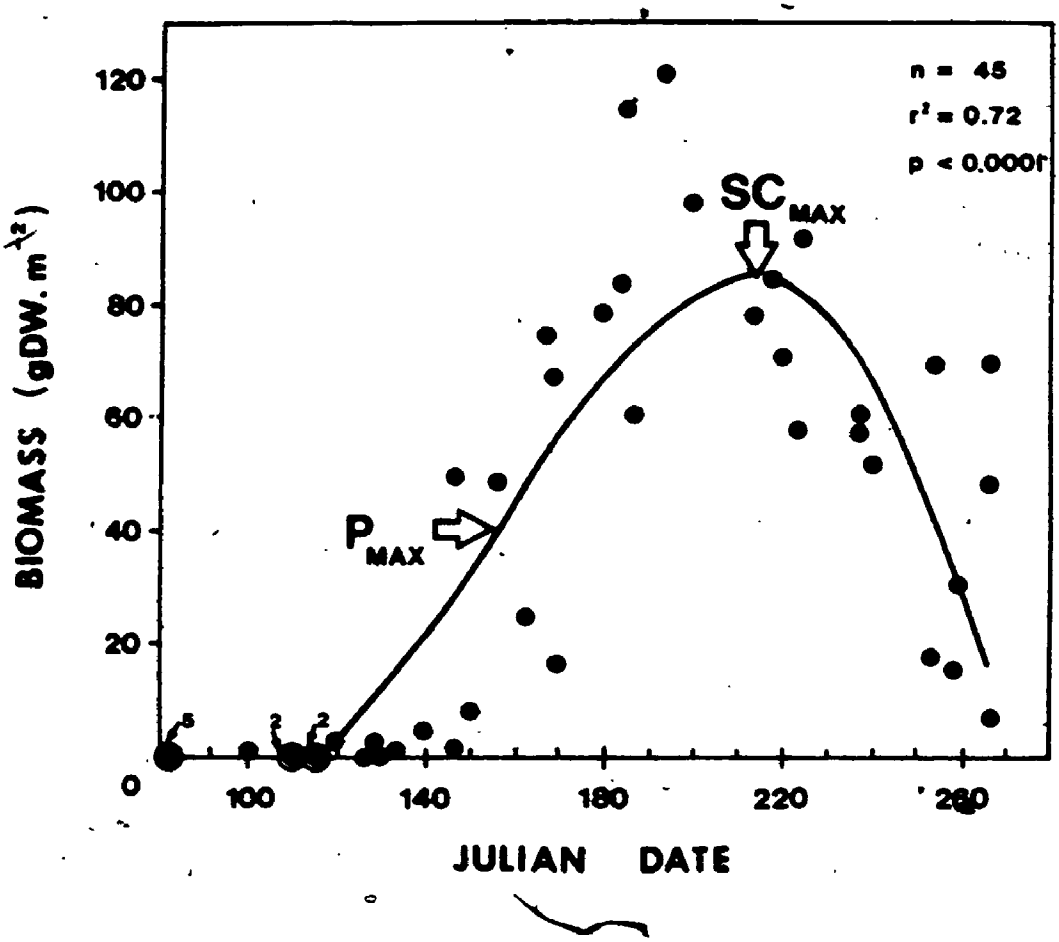

30 YEAR NORMAL
TEMPERATURE (°C)
16
12
8
4
0
-4
-8
-12
-16
DEPTH OF SNOW (cm)
8
6
4
2
0
A S O N D J F M A M J J A S O N D J F M A M J J A S
1984
1985
1986

FIGURE 3.

Seasonal changes in biomass of green vegetation, mean temperature, and mean hours of daily sunshine during 1986. The biomass curve was fitted using polynomial regression: BIOMASS = 310 - 7.5(DATE) + 0.056(DATE)^2 - 1.2E-04(DATE)^3. Date of maximum standing crop (SC_{max}) was estimated by setting the first derivative of this equation to 0. The date of maximum production of biomass (P_{max}) estimated by setting the second derivative of the equation to 0 (Hunt 1982). ● indicates that 2 or more data points have been superimposed.


n = 45
r² = 0.72
p < 0.0001
SC MAX
P MAX
BIOMASS (gDW.m⁻²)
JULIAN DATE
0
20
40
60
80
100
120
100
140
180
220
260

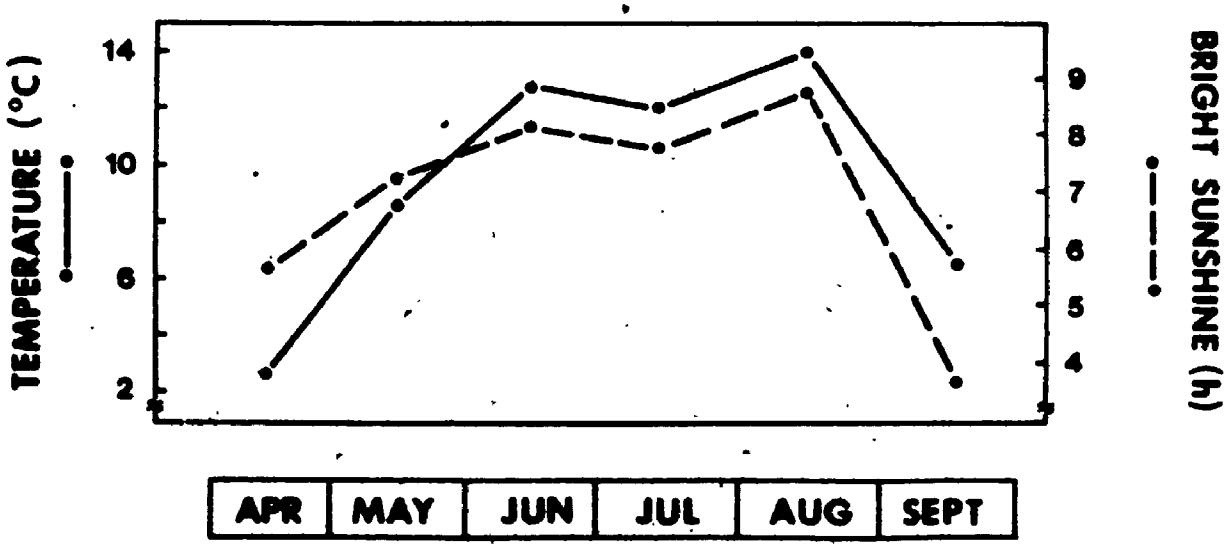

TEMPERATURE (°C)
BRIGHT SUNSHINE (h)
2
6
10
14
4
5
6
7
8
9
APR
MAY
JUN
JUL
AUG
SEPT

FIGURE 4.

Food consumption by breeding and non-breeding female bushy-tails in captivity, fed ad libitum. Weeks since conception were estimated by backdating from date of parturition, assuming a gestation period of 30 days (Egoscue 1962). The proportion of solid food that was directly consumed by nestlings was estimated from faecal production (see text for details). Means presented ±1 standard error.

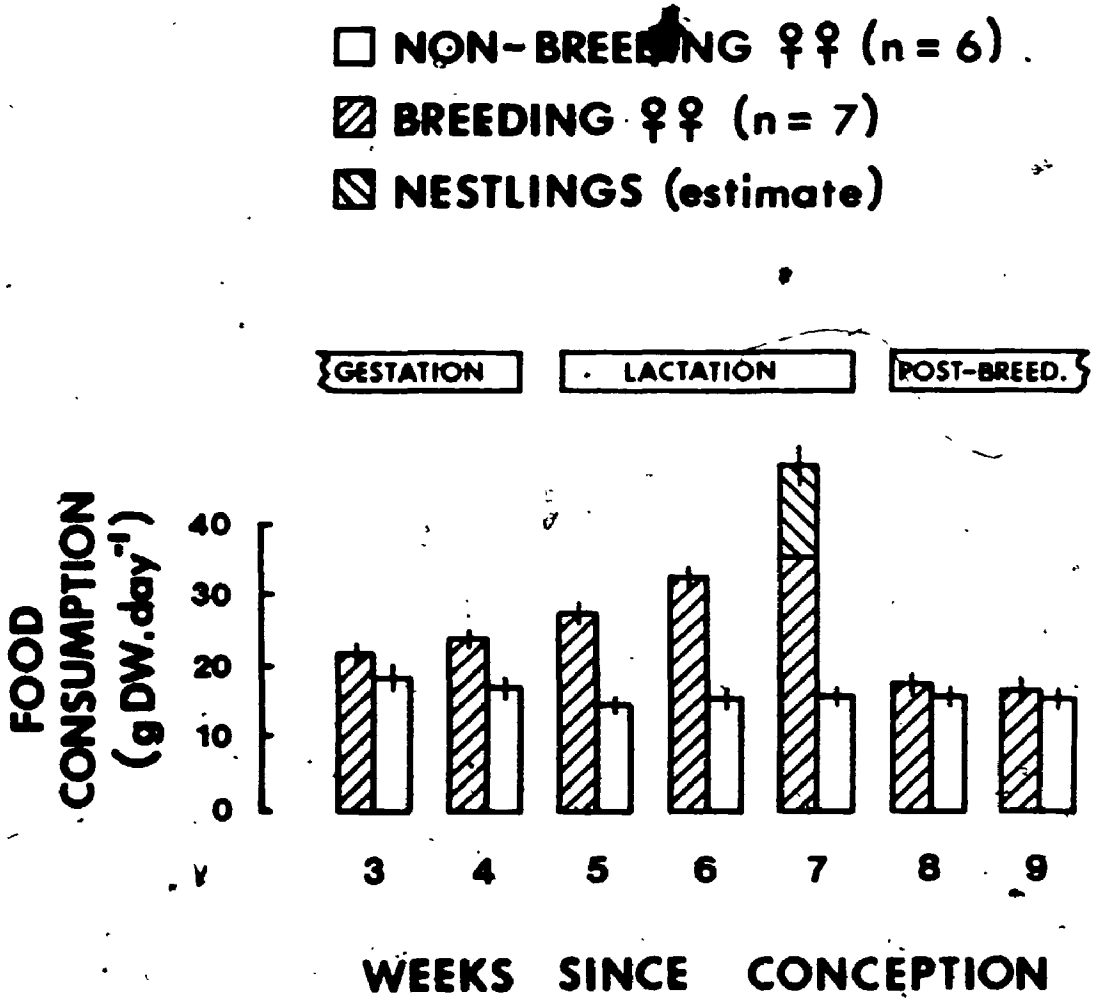

NON-BREEDING ♀♀ (n = 6)
BREEDING ♀♀ (n = 7)
NESTLINGS (estimate)
GESTATION
LACTATION
POST-BREED.
FOOD CONSUMPTION (g DW.day⁻¹)
40
30
20
10
0
3
4
5
6
7
8
9
WEEKS SINCE CONCEPTION

FIGURE 5.

Monomolecular growth curves for free-ranging bushy-tails on control and fed areas. Juveniles weaned before July 1 were classified as spring-cohort; those weaned later were classified as summer-cohort. Age was estimated assuming weight at 23 days of age to be 92 g for females and 103 g for males (lower dashed lines, see text for details). The upper dashed lines indicate mean adult weight on control areas. Weight increments did not differ significantly between control and fed areas for summer-cohort males (ANCOVA; $F=0.69$, $p=0.42$) and these data were pooled. Parameters and sample size for each growth curve are given in Appendix IV.

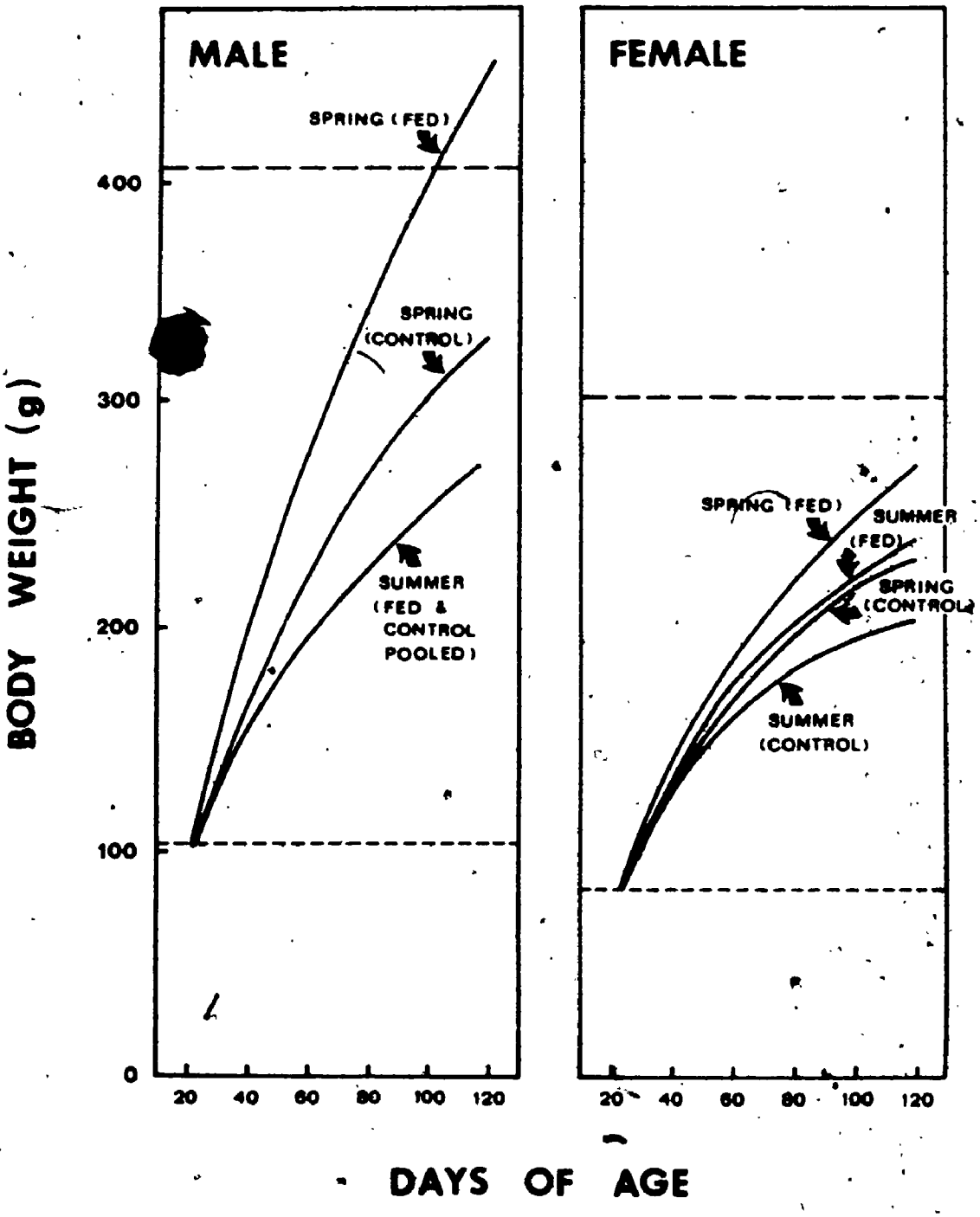

MALE
FEMALE
SPRING (FED)
SPRING (CONTROL)
SUMMER (FED & CONTROL POOLED)
SUMMER (FED)
SPRING (CONTROL)
SUMMER (CONTROL)
BODY WEIGHT (g)
0
100
200
300
400
20
40
60
80
100
120
DAYS OF AGE

FIGURE 6.

Influence of female body weight on date of first parturition. Pre-breeding weight was estimated as the weight of non-perforate females trapped on control areas during the period 15 April through 15 May in 1985 and 1986. Date of parturition was corrected for significant between-year variation in parturition date by subtracting 4.6 days from dates in 1985 and adding 4.6 days to dates in 1986 (see text for details).

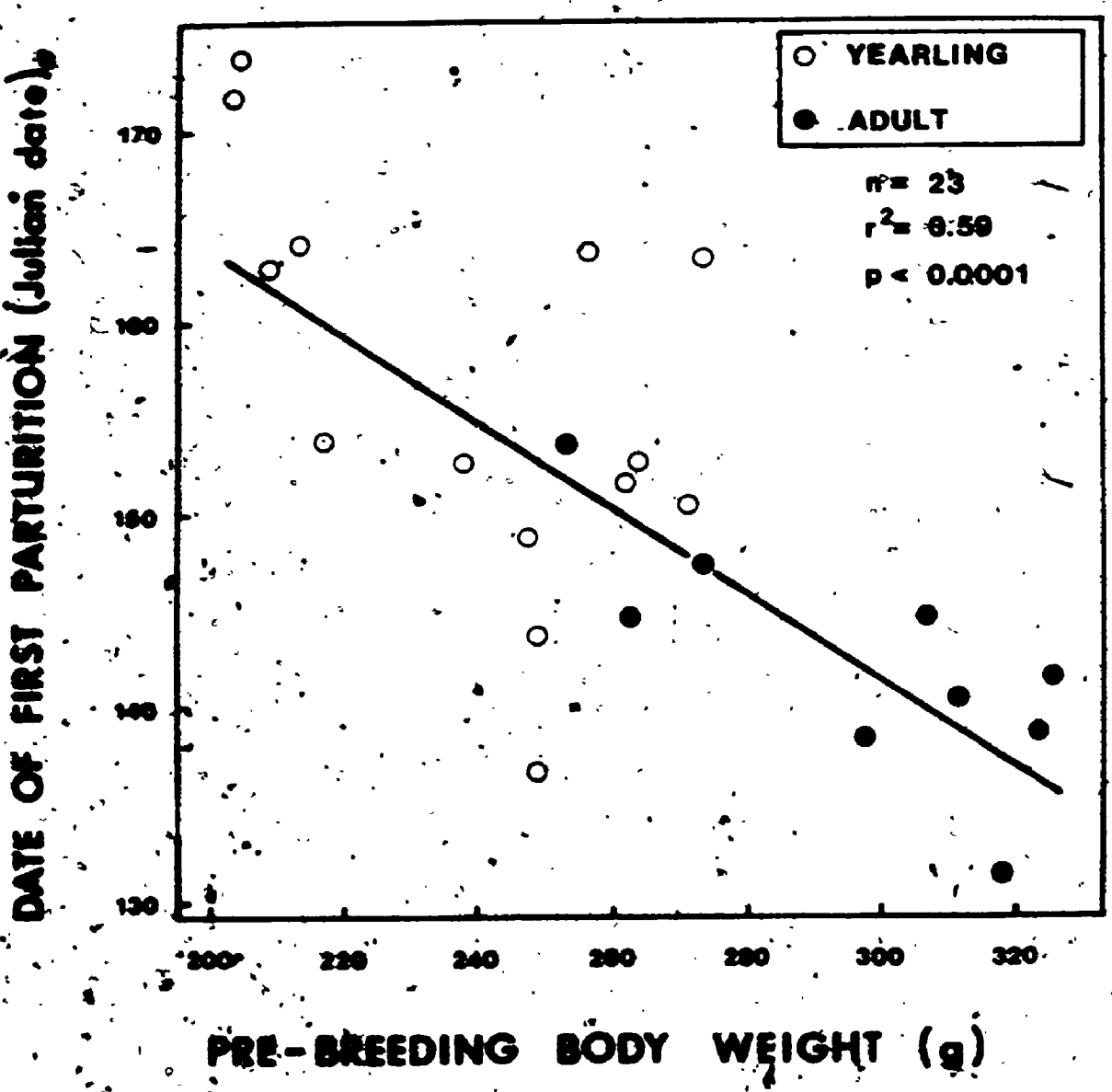
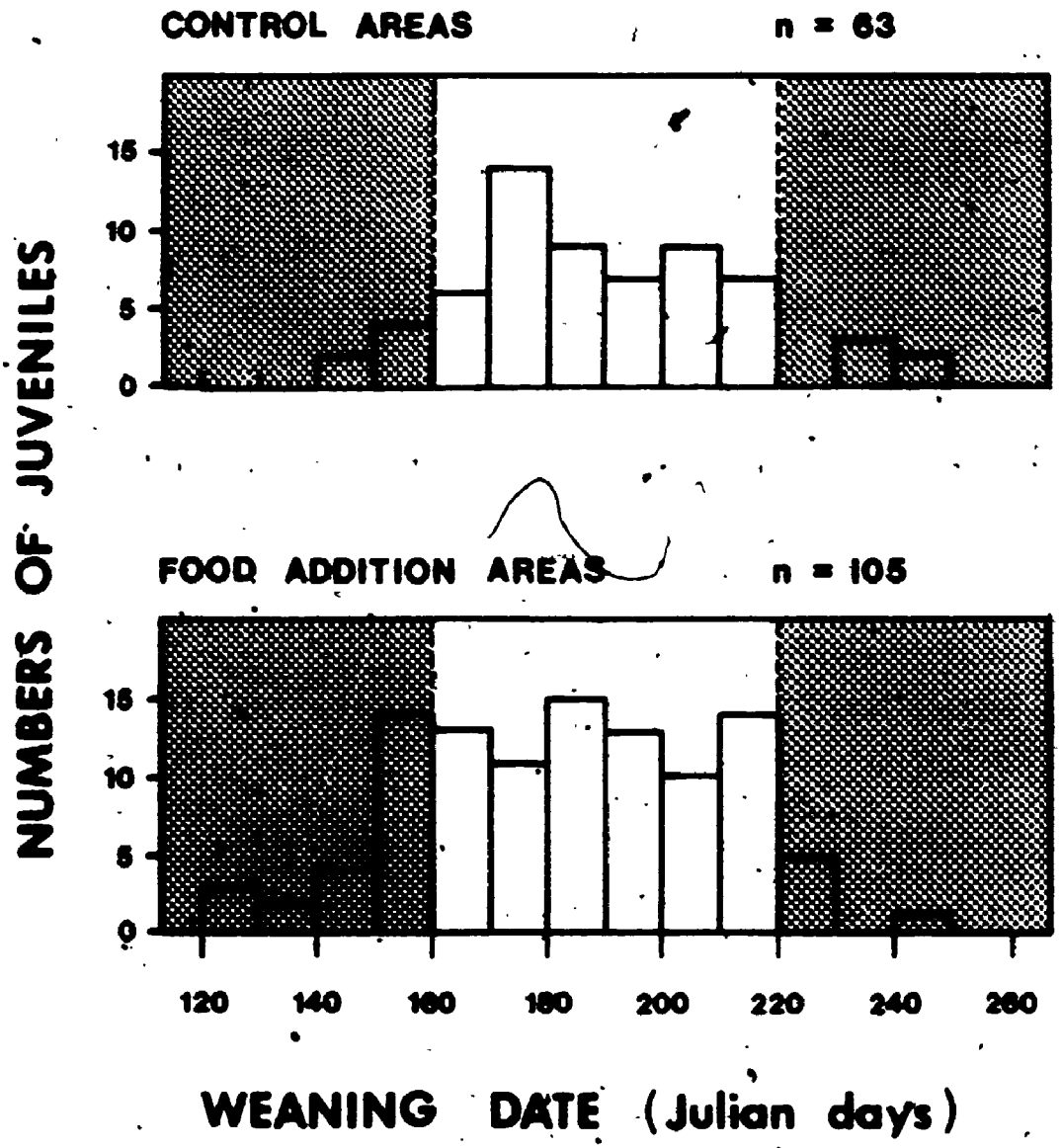

YEARLING
ADULT
n= 23
r²= 0.59
p < 0.0001
DATE OF FIRST PARTURITION (Julian date)
120
160
200
220
240
260
280
300
320
PRE-BREEDING BODY WEIGHT (g)

FIGURE 7.

Seasonal patterns of weaning on control and fed areas in 1986. Date of weaning was estimated from juvenile weight at first capture (see text for details). The unshaded area indicates the period of maximum food availability, defined as the interval between maximum production of green vegetation (P_{max}) and maximum above-ground standing crop (SC_{max}).


CONTROL AREAS
n = 63
FOOD ADDITION AREAS
n = 105
NUMBERS OF JUVENILES
0
5
10
15
120
140
160
180
200
220
240
260
WEANING DATE (Julian days)

3.4. Discussion

Herbivores faced with reduced food abundance may forage less selectively in order to maintain an adequate rate of forage consumption (Sinclair et al. 1982). Kill-trapped bushy-tails consumed 56% less forage prior to capture in winter than in summer, and the digestibility of their diet was 15% lower in winter than in summer. These results suggest that bushy-tails included low-quality food items in their diet during winter to compensate for a seasonal reduction in the availability of forage. In contrast, Wallage-Drees (1983) found no seasonal variation in the digestibility of rabbit (Oryctolagus) stomach contents, and Sadleir et al. (1973) found no seasonal variation in caloric or nitrogen content of Peromyscus stomach contents.

During summer, the digestibility of bushy-tail stomach contents (71% cell solubles) was lower than that of stomach contents from several other sympatric rodents (e.g. Peromyscus maniculatus 85%; Clethrionomys gapperi 84%; Millar unpubl.). Bushy-tails have a large caecum and large intestine relative to their body mass (Schieck and Millar 1985), which is likely an adaptation allowing bushy-tails to process relatively low-quality vegetation effectively. Neutral detergent analysis of the supplemental food used during this experiment indicated that Purina® Rat Chow (82% cell solubles) was a high-quality dietary supplement for bushy-tails but that alfalfa hay (56% cell solubles) was a low-quality food relative to their natural diet. This likely explains why bushy-tails made little use of hay during these experiments.

Body weight of captive females fed ad libitum declined by an average of 23 g (8%) between summer and winter. Iverson and Turner (1974) suggested that winter weight loss is characteristic of small non-hibernating mammals in boreal environments. They found that timing of weight variation in free-ranging Microtus pennsylvanicus was not directly related to seasonal variation in food abundance, and suggested that shortage of food was not a proximate cause of winter weight loss. Winter weight loss in non-hibernating herbivores may occur as part of an endogenous annual cycle, whereby non-storage tissue is reduced to minimize metabolic requirements during winter (Moen and Severinghaus 1981; Stebbins 1977; Steinlechner et al. 1983).

Free-ranging bushy-tails began to lose weight in early fall. As fat levels were high during winter, this weight loss indicates that either fat-free dry weight or water content was being reduced during fall in preparation for winter. Necropsy of bushy-tails suggested that fat-free dry mass did decrease during winter, although the seasonal difference was not statistically significant.

Loss of weight by captive bushy-tails during winter was associated with a decrease in their daily consumption relative to summer, which supports the hypothesis that weight loss is a mechanism for reducing metabolic requirements. However, food consumption by small mammals during winter may also be influenced by changes in activity (Stebbins 1977), body insulation (Steinlechner et al. 1983) and nest insulation (Brown 1968; pers. obs.). Experiments on Djungarian hamsters (Phodopus sungorus: Steinlechner et al. 1983) suggested that the onset of fall weight loss was triggered for this species by reduced daylength; whereas weight gain in spring was

controlled by an endogenous circannual rhythm. Seasonal weight changes in bushy-tails may be controlled in a similar manner.

Free-ranging bushy-tails had large fat reserves during winter, when forage availability and quality was low. The period of nutritional support potentially available to females from their endogenous reserves was about 3 days during winter. This indicated that endogenous reserves would be of little consequence for overwinter survival if bushy-tails were unable to obtain food for extended periods of time. Whittaker and Thomas (1983) estimated that snowshoe hares in Ontario had about 4 days of reserves during winter, which increased to about 6 days in summer. In contrast, the reserves of non-breeding bushy-tails during summer were equivalent to less than 2 days of nutritional support, and this fell to less than 1 day during lactation. Although these results suggest that bushy-tails are less likely to be nutritionally stressed in summer than in winter (Gyug and Millar 1980), they also demonstrate the necessity for bushy-tails to forage frequently in order to support the nutritional demands of reproduction.

Total daily consumption of lactating bushy-tails was about double that of non-breeding females. A doubling of food consumption during lactation is characteristic of a number of species of small mammals (Randolph et al. 1977; Schierwater and Klingel 1986). Mass of stomach contents was not influenced by reproduction, which suggests that the rate at which a female bushy-tail can obtain forage is primarily determined by forage abundance rather than by her nutritional requirements. If this interpretation is correct, then time spent foraging must increase during lactation. I know of no quantitative

data regarding activity patterns of woodrats during reproduction, but Harland and Millar (1980) noted a 77% increase in foraging time of lactating Peromyscus leucopus relative to non-breeding females. Equivalent data for bushy-tails could potentially be confounded if lactating females supplement their daily foraging by consuming food which they had stored in the den prior to lactation (see Appendix II).

Endogenous reserves were used to supplement daily foraging during reproduction. Fat levels were high during pregnancy and low during lactation. If body composition of adults and nestlings was similar, and the conversion efficiency of endogenous reserves was high, then depletion of stored energy during lactation (about 270 kJ) would be equivalent to 23% of juvenile production during lactation (P_L). There is considerable interspecific variation among small mammals in the use of metabolic reserves to support the nutritional demands of lactation; estimated values of P_L range from 84% in cotton rats (Sigmodon hispidus: Randolph et al. 1977), through 34% in arctic ground squirrels (Spermophilus parryii: Kiell and Millar 1980), to about 8% in white-footed mice (Peromyscus leucopus: Millar 1975). Interspecific variation in the use of endogenous reserves during lactation may, in part, relate to the allometric relationship between body weight and fat reserves that is apparent among species (Linsett and Boyce 1985). However, the marked difference in P_L between Sigmodon and Neotoma suggests that factors other than body weight also influence the relative use of endogenous reserves. Endogenous reserves are likely to be of greatest significance for species in unpredictable environments, for those experiencing high levels of predation, and for those that do not exhibit food caching (Randolph et al. 1977). Cotton rats do not

cache food (Dewsbury 1970) whereas bushy-tails are prodigious hoarders (Appendix II). Thus, differences in hoarding behaviour may partly explain the greater use of body reserves during lactation by Sigmodon than by Neotoma.

Prior to weaning, nestlings began to consume solid food which had been brought into the nest by their mother. This pattern of weaning may be adaptive in reducing the energetic demands on breeding females, which may be critical for females supporting embryonic growth of the second litter while suckling their first litter. In addition, providing the nestlings with solid food may delay their emergence from the den, and thereby reduce their susceptibility to predation.

Female bushy-tails generally timed the onset of breeding in such a manner that lactation coincided with the period of maximum food availability. There was, however, individual variation in onset of breeding. Much of this breeding asynchrony was related to body weight, with heavy females tending to initiate reproduction early in the season. If large energy reserves reduce the risk of reproductive failure for females which attempt to breed early in the season, then the positive correlation observed between body weight and fat content may explain the relationship between onset of breeding and female body weight.

Analysis of post-weaning growth patterns demonstrated an advantage to heavy females of having their first litters early in the season. Juveniles born early in the season not only had a longer period available for growth before winter than late season juveniles, but also grew faster than late season juveniles. Slade et al. (1984) found that seasonal growth rates of juvenile cotton rats (Sigmodon

hispidus) declined in a similar manner and they attributed this decline to a progressive reduction in forage digestibility during the season.

The bushy-tails of the Kananaskis Valley are the northernmost population of the genus Neotoma for which detailed estimates of life-history parameters are currently available (Appendix III). Slade et al. (1984) noted that Sigmodon exhibits more rapid growth at high latitudes than at low latitudes. In contrast, the growth rates that I estimated for bushy-tails on control areas in the Kananaskis Valley were similar to rates reported for more southerly populations. On control areas, mean growth rates for the first 60 days after birth averaged 3.4 $g \cdot day^{-1}$ for spring-cohort males, and 2.8 $g \cdot day^{-1}$ for spring-cohort females. These data are similar to growth rates for captive bushy-tails in Utah (3.6 $g \cdot day^{-1}$ for males and 2.6 $g \cdot day^{-1}$ for females: Egoscue 1962), for captive and free-ranging bushy-tails in California (3.0 $g \cdot day^{-1}$ for males and 2.8 $g \cdot day^{-1}$ for females: Escherich 1981), and for free-ranging bushy-tails in Idaho (3.6 $g \cdot day^{-1}$ for males and 2.8 $g \cdot day^{-1}$ for females: Martin 1973). However, I recorded growth rates for spring-cohort juveniles on the fed areas (4.1 $g \cdot day^{-1}$ for males and 3.1 $g.day^{-1}$ for females) that were higher than any rates previously reported for this species.

McClure and Randolph (1980) noted that growth of male woodrats (N. floridana) was more variable than growth of females. These authors postulated that there is strong selection for large male body size in this genus due to subsequent advantages in aggressive interactions. However, these advantages may be counteracted by males being more susceptible than females to the effects of restricted food abundance.

My results support this hypothesis as there was greater seasonal variation in male growth rate than female growth rate, and food addition had a greater effect on male growth than female growth.

An additional advantage to breeding early in the season was that early breeders were more likely than late breeders to produce a second litter. Unlike small mammals that hibernate, a number of non-hibernators produce 2 litters (e.g. Ochotona princeps: Millar 1974; Smith and Ivins 1983a) or several litters (e.g. Peromyscus maniculatus: Millar and Innes 1983; Lepus americanus: Vaughan and Keith 1981) each season. Escherich (1981) reported that bushy-tails began breeding in February in the Sierra Nevada Mountains, where they produced up to 3 litters per season. I recorded a maximum of two litters per season for bushy-tails in the Kananaskis Valley, which suggested that a short season of primary production has constrained the maximum number of litters per season that can be successfully weaned by bushy-tails in this area. Pikas (Ochotona princeps) frequently produce 2 litters in a season but are rarely successful in raising both litters to independence (Millar 1974; Smith and Ivins 1983a). In contrast, bushy-tails which bred twice during a season were usually successful in weaning juveniles from both litters.

Mean litter size during gestation, and at parturition, ranged from 3 to 5 among bushy-tails in the Kananaskis Valley. Egoscue (1962) and Escherich (1981) both reported a number of cases where litter size at birth was 1 or 2 for captive bushy-tails. However, Escherich noted that litter size declined with increasing time in captivity, and the estimates of litter size given by these authors may not be representative of free-ranging populations.

Bushy-tails on fed areas were heavier and bred earlier than bushy-tails on control areas. This finding was consistent with a number of other food supplement experiments which demonstrated that addition of food during winter resulted in increased body weight and earlier initiation of reproduction (Taitt 1981; Taitt and Krebs 1981; Vaughan and Keith 1981; Wallage-Drees 1983; Watts 1970; but see Sullivan and Sullivan 1982). The mild 1985/86 winter had reduced snow-cover in spring, and this influence on the onset of breeding was similar to that caused by the addition of supplemental food. It is clear that the probability of a female producing a second litter was related to how early she initiated breeding. Thus, the proportion of females having 2 litters was influenced both by food addition and by variation in climate between years, since both had similar effects on onset of breeding. In contrast, litter size at weaning was influenced by food addition, but did not vary between years. This suggests that weaning success is influenced by food abundance but is not strongly influenced by yearly variation in the timing of primary production.

In conclusion, the observed seasonal patterns in energy reserves, reproduction, and growth were consistent with the hypothesis that bushy-tails experience seasonal shortages of food. Food is clearly an important ultimate limit to the seasonal pattern of reproduction in this species. Furthermore, the experimental addition of food resulted in significant increases in reproductive output and post-weaning growth. This demonstrated that food also acts as a proximate limit to bushy-tail reproduction and growth. The effect of food addition on the pattern of seasonal reproduction exhibited by bushy-tails was, however, relatively slight. Although the onset of breeding was about

one month earlier on fed areas in 1986 than on control areas in 1985, food addition did not result in winter breeding, breeding by young of the year, or the production of more than 2 litters during a single breeding season. Thus, the general pattern of seasonal reproduction exhibited only a limited degree of phenotypic plasticity. This plasticity allowed females to fine-tune their breeding response in relation to the specific environmental conditions that occurred during each breeding season.

CHAPTER FOUR - GROUP DYNAMICS

4.1. Introduction

The hypothesis of resource defense polygyny (Emlen and Oring 1977) proposes that territorial males exclude other males from patches of suitable breeding habitat and thereby monopolize the females inhabiting these patches. The mating success of territorial males is determined by female choice on the basis of territory quality (Orians 1969; Wittenberger 1980). For species which exhibit little paternal care, territory quality may be determined by the level of physical resources such as den sites, or food, within the area defended by each male (Wittenberger 1980).

If females aggregate within male territories to gain access to some critical resource, then the number of females in a resource defence polygynous group is likely limited by the cost of competition among group members for this resource (Wittenberger 1980). That is, female group size should be limited at the point where any additional female which joined the group would experience reduced reproductive success as a result of competitive interactions with other group members.

Resource defense polygyny has been proposed as an explanation for polygyny in woodrats (N. lepida: Vaughan and Schwartz 1980; N. stephensi: Ward 1984), and is consistent with the pattern of harem-polygyny reported for N. cinerea (Escherich 1981). Several authors have suggested or implied that resource defence polygyny represents a convergent form of social organization among species of

small mammal which inhabit discontinuous patches of rocky habitat (Mares and Lacher 1986; Orians 1969; Wittenberger 1980).

Although Escherich (1981) proposed that bushy-tails exhibit a polygynous mating system, this conclusion was drawn primarily from an analysis of age structures and sex ratios among museum collections of bushy-tails. Escherich also monitored 4 small groups of bushy-tails in the Sierra Nevada Mountains using live-trapping and limited radio-telemetry. However, 3 of these areas did not have permanent settlements of bushy-tails present during each year of the study (1970-1974). Furthermore, Escherich determined group composition from June through August, and thus did not provide direct evidence of group structure during the mating season, which in this area began during March or April.

I determined the size and composition of 16 groups of bushy-tails in the Kananaskis Valley during the mating season in order to test the following hypothesis:

Hā: Bushy-tails in the Kananaskis Valley exhibit resource defence polygyny (sensu Emlen and Oring 1977).

The hypothesis of resource defence polygyny generates a number of predictions regarding the group dynamics which should characterize bushy-tails living in patchy habitat.

For resource defence to operate as an effective mating strategy, critical resources must be defensible by territorial males. Thus, resource defence polygyny requires that resources be patchily

each bushy-tail be closely associated with a patch of habitat, at least for the duration of the breeding season.

There should be variation in group sex ratio in relation to size of habitat patch. Monogamous pairs of bushy-tails should be most common on small patches of habitat, whereas varying degrees of polygyny should be found on larger patches (Downhower and Armitage 1971; Orians 1969).

Philopatry (defined as an individual breeding on its natal patch of habitat) should be more common among females than among males, because intrasexual aggression likely prevents young males from becoming resident within the territory of a dominant male (Dobson 1982; Moore and Ali 1984).

Trivers and Willard (1973) proposed that breeding females in good physiological condition should invest preferentially in the offspring sex that would receive the greatest benefit from that investment. There are limited opportunities for post-weaning investment in male offspring in a polygynous system, because juvenile males tend to disperse soon after weaning (Greenwood 1980). However, allowing a juvenile female to share the natal home range may constitute a substantial post-weaning investment by breeding females (Armitage 1981; Clutton-Brock and Albon 1982). A breeding female has the option of allowing female offspring born early in the season to share the maternal home, which would ensure that these offspring obtained habitat which had already proven successful by the survival and reproduction of the mother (Michener 1983). Alternatively, delaying investment in female offspring until late in the season should reduce local resource competition (Clark 1978; Silk 1983) between a breeding

female and her offspring while the female reared a second litter (because a male-biased first litter would be more likely to disperse). If a breeding female adopted either of these options, then the proportion of female juveniles which were philopatric would vary seasonally. Seasonal variation in opportunities for offspring philopatry might consequently favour seasonal variation in sex ratio of offspring (e.g. Goundie and Vessey 1986; McShea and Madison 1986).

Summary of Predictions:

1) Breeding bushy-tails are closely associated with discrete patches of rocky habitat.
2) Female group size on these patches is variable, resulting in varying levels of polygyny being observed within the population.
3) Females are more likely to be philopatric than males.
4) There is seasonal variation in the probability of a female juvenile being philopatric.
5) Sex ratio of offspring varies seasonally.

For resource defence polygyny to function as an effective mating strategy for males, there must be a tendency for females to become grouped on patches of habitat so as to gain access to some critical resource. If the abundance of this resource determines the level of competition within the groups, then changes in resource levels should influence female group size and, consequently, the level of polygyny exhibited by territorial males. Chapter 3 provides direct evidence that food abundance limits reproduction and growth of bushy-tails. Therefore, I propose that food is a critical resource for female

bushy-tails, and that group size in this species is proximately limited by competition among females for food.

Mares et al. (1976, 1982) found that supplemental food increased the density of a population of chipmunks (Tamias striatus) by decreasing home range size, thereby allowing additional individuals to settle on the fed area. If female bushy-tails exhibit spacing behaviour as a proximate response to intrasexual competition for food, then addition of food should result in increased group size through reduced female spacing behaviour (cf. Taitt 1981). Food addition may thereby increase the potential for polygyny within groups of bushy-tails living on patches of rocky habitat. I tested the following hypothesis:

Ha: Addition of food increases female group size and, therefore, the level of polygyny exhibited by territorial male bushy-tails.

Specific predictions arising from this hypothesis are listed below. If female bushy-tails exhibit spacing behaviour as a proximate response to intraspecific competition for food (Mares et al. 1976, 1982; Taitt 1981), there should be a decrease in female home range size and an increase in the number of breeding females on supplementally fed areas. If male spacing behaviour is primarily related to competition for mates (Dobson 1982; Moore and Ali 1984), then dominant males should continue to exclude other males from supplementally fed areas. Thus, food addition should have no direct effect on male home range size or the number of breeding males.

A polygyny threshold (sensu Willson 1966) exists if differences

in resource quality among habitat patches result in females becoming resident on habitat patches already occupied by female(s) in preference to patches defended by unmated males (Orians 1969). If a polygyny threshold related to food availability exists for bushy-tails there should be increased immigration of females onto fed areas relative to control areas.

Supplemental food has been shown to increase the survival of some small mammals (Dobson and Kjelgaard 1985; Ford and Pitelka 1984; Sullivan and Sullivan 1982; Taitt 1981; but see Gilbert and Krebs 1981; Taitt and Krebs 1981). If forage availability directly limits the survival of juvenile or overwintered bushy-tails, then survival rates should be higher on fed areas than on control areas.

If dispersal occurs as a response to intraspecific competition for food (Boutin 1984; Taitt 1981), there should be increased levels of philopatry exhibited by bushy-tails on fed areas relative to control areas.

Reproductive success is more variable for males than for females in polygynous species (Trivers 1972), and male success is likely related to body mass (Erlinge 1977; Trivers and Willard 1973). If females on fed areas have large energy reserves, then Trivers and Willard (1973) predict that these females will preferentially invest in male offspring (because male offspring are more likely to benefit from high levels of maternal investment during gestation and lactation than are female offspring). Clutton-Brock et al. (1985) predict a similar relationship between maternal energy reserves and sex ratio of offspring, although their hypothesis is based on differential rates of juvenile mortality, rather than differential parental investment.

Summary of Predictions:

1) Female home range is smaller on fed areas than control areas.
2) Food addition will increase the number of breeding females but will have no direct effect on the number of breeding males.
3) There is greater immigration of females onto fed areas than control areas.
4) There is greater survival of females on fed areas than control areas.
5) Juveniles are more likely to be philopatric on fed areas than control areas.
6) A greater proportion of male offspring is weaned on fed areas than control areas.

4.2. Methods

4.2.1. Home range.

Woodrats exhibit movement patterns which violate the distributional assumptions of probabilistic models for estimating home range size (N. fuscipes: Wallen 1982), and bushy-tail home ranges were irregularly shaped in the rugged habitat of the Kananaskis Valley (pers. obs.). However, home range estimates based on distance moved between capture locations avoid assumptions regarding home range shape (Slade and Swihart 1983). I calculated the natural logarithm of mean distance travelled by individual bushy-tails between live-trap captures (logD; modified from Davis 1953; Koeppl 1977) as an index of home range size. For each recapture, I calculated the shortest horizontal distance between the capture location and the previous 2

capture locations of that individual. Aerial photographs (original scale 1:20000, enlarged to 1:4000) were used to determine trapsite coordinates. By estimating distances between pairs of points for which the exact separation was known, I determined that this technique provided an accuracy of about ±2 m for movements of less than 100 m, and ±5 m for movements over longer distances. The 2 previous trap locations were incorporated into the analysis to avoid over-representing occasional long-distance movements, and natural logarithms were used to normalize the variance of the index.

To increase sample size, I included movement data from live-trapping in areas other than the fed and control areas. These data were pooled with data for the control areas. A two-way ANOVA was used to determine the influence of sex and food addition on home range size during the breeding season, and a one-way ANOVA was used to investigate seasonal variation in home range from May through September.

4.2.2. Population trends.

I used the minimum number of animals known to be alive on the trapping areas (MNA) to assess overall population trends on the trapping areas. MNA provides an adequate measure of population trends provided minimum trappability exceeds 50% (Hilborn et al. 1976).

4.2.3. Group size.

Group size was defined as the number of breeding residents on each trapping area (after Wittenberger 1980, but see Jarman 1982 for an alternative definition). Residents of an area were defined as

overwintered individuals that were live-trapped on that area on 3 or more occasions, and that had a trappability of at least 50%. Overwintered bushy-tails that were less than 50% trappable, and those not captured on at least 3 occasions in an area, were classified as transients.

Trappability is a measure of the probability that an individual bushy-tail will be captured during a trapping session. I calculated trappability as a minimum unweighted estimate, excluding first and last captures (Hilborn et al. 1976).

Residents were classified as breeding if they were captured in reproductive condition before 1 July. (The mean date of last parturition by breeding females fell during the first week of July in both 1985 and 1986, and did not vary between control and fed areas; $t=0.09$, $p=0.9$). Males with scrotal testes, and females that were pregnant or lactating, were considered to be in reproductive condition. Overwintered bushy-tails were classified as yearling or adult, as described in 3.2.6.

Spearman rank correlation was used to determine the relationship between size of habitat patch and number of resident bushy-tails. The horizontal length of exposed rock, measured from aerial photographs, was used as a measure of patch size. Two-way ANOVA was used to determine the influence of year and food addition on numbers of male and female residents and the sex ratio of overwintered bushy-tails on each of the fed and control areas. Body weight, scent gland activity, and wounding rates were compared between classes of resident and transient males using a Kruskal-Wallis nonparametric ANOVA. The relative proportion of individuals that were known to be yearlings was

compared between areas using a contingency table chi-square analysis.

4.2.4. Philopatry, immigration, and dispersal.

Juveniles caught within 50 days of their estimated date of weaning were assumed to have been born on the trapping area where they were first captured. Juveniles caught after this period were classified as probable immigrants. Non-immigrant juveniles which subsequently bred on their putative natal area were classified as being philopatric (after Greenwood 1980).

Females exhibited variation in the timing of their first parturition (Chapter 3) and it was not possible to unambiguously classify juveniles as being from first or second litters. In order to determine the influence of season on philopatry, I separated juveniles into early- and late-season cohorts on the basis of estimated date of birth. The dividing date between cohorts was taken as 25 days after the date of first parturition on each trapping area (estimated as the mean of the earliest 2 dates of birth among the juveniles captured on that area). Date of birth was estimated from weight at first capture, as described in 3.2.5. As gestation lasts about 30 days (Egoscue 1962), a 25-day demarcation of early and late cohorts ensured that most first litter juveniles, and no second litter juveniles, would be assigned to the early cohort.

Overwintered bushy-tails were classified as immigrants if they were not caught during the first 3 trapping sessions in an area but subsequently appeared and became resident on that habitat patch. Five removal areas were kill-trapped on 3 separate occasions during 1984 to remove adult residents. These areas were then live-trapped regularly

during 1985 and 1986 to monitor recolonization of this vacant habitat.

4.2.5. Survival.

It was not possible to determine whether residents which disappeared from an area had emigrated, or had died. Therefore, I did not distinguish between emigration and mortality when estimating the survival of juveniles and adults.

Three-way log-linear analysis was used to determine the influence of year and food addition on the proportions of resident adults and philopatric juveniles in 1985 which survived and bred during the 1986 breeding season.

4.2.6. Sex ratio of offspring.

It was not possible to gain access to juveniles while they were in their natal dens. I calculated the sex ratio of juveniles captured on their putative natal area (i.e. excluding probable immigrants) and assumed that this was an accurate estimate of sex ratio at weaning. These estimates could be biased by differential mortality or dispersal of recently weaned juveniles, and should be interpreted with caution.

The influence of year, season, and food addition on sex ratio of offspring was determined using log-linear analyses, with early- and late-season cohorts defined as in 4.2.4.

4.3. Results

4.3.1. Home range.

Overwintered male bushy-tails had significantly larger

home ranges than overwintered females during the breeding season (Table 12. Two-way ANOVA; $F=24.9$, $p<0.0001$). Food addition did not affect the home range of either sex ($F=1.4$, $p=0.24$). There was significant seasonal variation in male home range size from May through September (Figure 8. One-way ANOVA; $F=4.4$, $p<0.005$), whereas female home range size did not vary seasonally ($F=0.92$, $p=0.5$).

For 12 of the 16 control and fed areas, the nearest adjacent rocky habitat was regularly live-trapped during the study. An examination of these trapping records indicated that a number of bushy-tails moved among adjacent trapping areas. The median length of the patches of rocky habitat was 130 m (range 8-320 m) and the median distance between trapped areas and the closest adjacent rocky habitat was 350 m (range 90-1920 m). There were only 3 records of adult females moving further than 350 m between captures; these comprised 0.6% of total movements recorded for adult females (n=540). In contrast, 10% (28 of 307) of adult male movements exceeded 350 m; this difference between the sexes was highly significant (Fisher Exact test, $p<0.0001$).

4.3.2. Population trends.

Trappability of bushy-tails was high (83%; n=181), and did not vary between control and fed areas (Mann-Whitney U-test, $p=0.4$), or between the sexes ($p=0.3$). Trappability was significantly higher for juveniles (86%; n=78) than for overwintered bushy-tails (82%; n=103, $p<0.02$). There was no evidence of any progressive decline in trappability among individuals that were captured repeatedly during the study. (A decline in trappability might have indicated that some

individuals were becoming trap-shy). No bushy-tails lost both eartags during the study, which allowed all recaptured individuals to be accurately identified.

Before investigating group dynamics, I examined overall population trends on control and fed areas for the period August 1984 through September 1986 (Figure 9). Five areas were not extensively trapped during 1984 and were excluded from this comparison. (Note that both resident and transient bushy-tails are included in estimates of minimum number alive). In August 1984, prior to the addition of supplemental food, a total of 41 adults (14 male:27 female) and 33 juveniles were captured on the 11 areas. The number of overwintered bushy-tails declined progressively during each season on the control and fed areas, but the minimum number of overwintered bushy-tails alive during August did not vary significantly among years (X^2=0.78, p=0.7; based on an expected value of equal numbers per year), despite the availability of supplemental food on the experimental areas during 1985 and 1986. Sex ratios of adults were also similar among years, ranging from 10 males:25 females in 1984 to 13 males:21 females in 1986.

The most obvious difference between areas was that more juveniles were present on fed areas than control areas from May through July in 1986.

4.3.3. Group size.

The average group of bushy-tails in the Kananaskis Valley consisted of a single overwintered male and 2 or 3 overwintered females with associated juveniles. No males were resident on 4 of the

areas in 1985, and 2 of the areas in 1986 (Table 13), although the resident females on these areas bred successfully. There were 5 records of male-female pairs during 1985, but only 1 area continued to have a male-female pair during 1986. The largest group consisted of 3 resident males and 5 resident females. Group sex ratio was female biased in 25 of 32 cases.

Group size was positively correlated with patch size (r_s=0.58, $p < 0.02$). However, both male and female numbers increased with increasing patch size (Figure 10) and there was no correlation between patch size and group sex ratio (r_s=0.29, p=0.31). Multiple residency of males was only observed on rock outcrops with a horizontal length of at least 150 m.

Group size differed between 1985 and 1986 on 13 of the 16 trapping areas (Appendix VI), but I found no significant trend in group size or group sex ratio between years, or between control and fed areas (Table 14).

The majority of resident males (26 of 34) did not move among trapping areas. The remaining 8 residents were recorded on 2 or more trapping areas during the breeding season. I classified the former males as "local" residents, and the latter as "roaming" residents. Roaming residents were heavier than local residents and transients, and had the highest frequency of visible wounds (Table 15). Local and roaming residents had active scent glands, whereas transients exhibited little scent gland activity (Table 15). The majority of transients were known-age yearlings, whereas few local residents and no roaming residents were known-age yearlings (Table 15).

Significantly more male than female non-residents (i.e. roamers

and transients) were recorded on the trapping areas (Table 16). The relative proportions of residents and non-residents did not vary significantly with either year or food addition.

4.3.4. Philopatry, immigration, and dispersal.

About half (30 of 56; 54%) of the breeding residents of known origin on fed and control areas in 1986 originated as philopatric juveniles from previous breeding seasons (Table 17); this proportion was identical on control and fed areas. However, the level of philopatry varied significantly between the sexes (71% for females, 17% for males; Fisher exact test, $p<0.001$).

Of 259 juveniles tagged on the control and fed areas, there were 19 records of tagged juveniles moving between trapping areas but only 1 record of a tagged juvenile (a male) becoming resident on a non-natal area. One tagged overwintered female became resident in a new area, having moved between Marmot and Castro (see Appendix I), which were separated by only 90 m.

Five areas were kill-trapped during 1984 to remove the resident population of bushy-tails, which totalled 5 adult males and 10 adult females. A total of 34 (23 males, 11 females) individuals appeared on these areas during 1985; the majority (68%) being juveniles which appeared during the late summer and early fall. Only 6 of these individuals (2 males, 4 females) became resident on the removal areas, and none bred there until the 1986 breeding season.

4.3.5. Survival.

Thirty-three percent (17 of 51) of breeding residents in 1985

remained on their resident area and bred in 1986 (Table 18a). This proportion did not differ between sexes (log-linear analysis; $X^2=0.06$, $p=0.8$). A similar proportion (26 of 80, 33%) of juveniles from the 1985 breeding season survived and bred on their natal area in 1986 (Table 18b). Juvenile females were more likely to survive than juvenile males ($X^2=5.27$, $p<0.05$). Food addition did not influence the survival of either residents or juveniles ($X^2=0.36$, $p=0.6$; $X^2=0.10$, $p=0.7$; respectively).

The proportion of female juveniles born during 1985 that survived to breed during 1986 varied significantly between the early-season cohort (20 of 36, 56%) and the late-season cohort (2 of 13, 15%; Fisher exact test, $p=0.05$).

Twelve areas had both male and female juvenile recruits in 1985; 9 of these had 1 or more philopatric juvenile females survive the winter and breed in 1986, whereas 2 had philopatric juvenile males surviving and I had no natal philopatry. In no case did both male and female juveniles remain philopatric on the same area.

4.3.6. Sex ratio of offspring.

A significantly higher proportion of male offspring was weaned on fed and control areas in 1986 than in 1985 (Table 19a. Log-linear analysis; $X^2=7.53$, $p<0.02$). There was no evidence of variation in sex ratio between fed and control areas ($X^2=0.01$, $p=0.9$). In both 1985 and 1986 there tended to be more females in the early-season cohort of offspring than the late-season cohort (Table 19b), although the difference was not statistically significant when the influence of between-year variation in sex ratio was removed ($X^2=2.26$, $p=0.13$).

Table 12. Mean home range indices for overwintered residents on fed and control areas from May through July in 1985 and 1986. A home range index was calculated for each individual that was live-trapped on 3 or more occasions. The index was calculated as the natural logarithm of the mean distance between locations of capture (see text for details). Means presented ± 1 standard error; sample size in parentheses. Variances were homogeneous (F_{max} test, $p>0.05$).

Sex	Area	Home Range Index (logD)
MALE	Control	3.82 ± 0.37 (22)
	Fed	3.80 ± 0.28 (12)
FEMALE	Control	2.34 ± 0.18 (45)
	Fed	2.78 ± 0.18 (29)

Table 13. Group size distributions for the 16 control and fed areas in 1985 and 1986. Group size was defined as the number of breeding residents on each area (after Wittenberger 1980).

		1985				1986			
	5	-	1	1	1	-	1	1	-
	4	-	-	1	-	-	-	1	-
No. of	3	-	1	-	-	-	4	2	-
females	2	-	2	-	-	1	3	-	-
	1	4	5	-	-	1	1	1	-
	0	-	-	-	-	-	-	-	-
		0	1	2	3	0	1	2	3
		No. of males							

Table 14. a) Numbers of male and female breeding residents, and group sex ratios (females per male) on control and fed areas. b) ANOVA table for the influence of year and food addition on a). Means are presented ±1 standard error. Variances were homogeneous (F_{max} test, $p>0.05$), and all two-way interactions were non-significant.

a) Year	Area	No.males	No.females	Sex ratio[1]
1985	Control	1.1 ± 0.2	2.3 ± 0.6	1.8 ± 0.3
	Fed	0.9 ± 0.3	2.1 ± 0.6	2.1 ± 0.7
1986	Control	1.1 ± 0.2	2.8 ± 0.5	2.5 ± 0.5
	Fed	1.3 ± 0.3	2.6 ± 0.4	2.1 ± 0.3

1. Excluding 6 cases where no male was resident during the breeding season,

b) TWO-WAY ANOVA:

	RESPONSE VARIABLE											
	No.males				No.females				Sex ratio[1]			
Source	df	SS	F	p	df	SS	F	p	df	SS	F	p
Year	1	0.28	0.50	ns	1	2.00	0.91	ns	1	0.81	0.60	ns
Food	1	0.03	0.06	ns	1	0.13	0.06	ns	1	0.01	0.01	ns
Error	29	16.41			29	63.75			23	31.14		
Total	31	16.72			31	65.88			25	31.97		

1. Excluding 6 cases where no male was resident during the breeding season.

Table 15. Comparison of body weight, scent gland activity, wounding, and age among 3 classes of overwintered male. Local residents did not move among trapping areas, whereas roaming residents were primarily captured on one area but were also captured on adjacent areas during the breeding season. Transient males were not consistently trapped on any one area during the breeding season. Means are presented ±1 standard error.

	Local resident (n=26)	Roaming resident (n=8)	Transient (n=14)	Kruskal-Wallis test
Body weight (g)	356 ± 10	455 ± 32	290 ± 9	H=22.6 p<0.0001
Scent gland activity index	52 ± 5	55 ± 11	16 ± 2	H=20.7 p<0.0001
No. of wounds	0.5 ± 0.2	1.1 ± 0.5	0.1 ± 0.1	H=7.5 p<0.05
				Chi-square test
Number known to be yearlings	9 (35%)	0 (0%)	11 (79%)	X^2=14.1 p<0.001

Table 16. Numbers of a) resident and non-resident overwintered females, and b) resident and non-resident overwintered males captured on each trapping area during the breeding season. c) Log-linear analysis for the influence of sex, year, and food addition on a) and b). Two- and three-way interactions were non-significant.

	1985		1986	
	Resident	Non-resident	Resident	Non-resident
a) Females				
Control areas	18	4	22	2
Fed areas	17	7	22	3
b) Males				
Control areas	9	6	9	7
Fed areas	7	7	10	6

c) LOG-LINEAR ANALYSIS

SOURCE	DF	CHI-SQ	PROB
Sex	1	11.45	$p < 0.001$
Year	1	1.96	ns
Food addition	1	0.53	ns

Table 17. Origin of residents present on control and fed areas during the 1986 breeding season. Philopatric individuals were resident on their putative natal area. Immigrants were defined as adults first caught after more than 3 trapping sessions in an area, and juveniles first caught more than 3 trapping sessions after their estimated date of weaning.

		NO. OF RESIDENTS DURING 1986	ORIGIN OF RESIDENTS		
			Unknown[1]	Philopatry	Immigration
Female	Control	22	3	12	7
	Fed	21	2	15	4
Male	Control	9	0	3	6
	Fed	10	1	0	9

1. Overwintered bushy-tails present when the areas were first trapped in 1984.

Table 18. Survival of a) overwintered residents and b) juveniles from the 1985 breeding season until the 1986 breeding season.

a) OVERWINTERED RESIDENTS:

Sex	Area	No. of individuals Resident'85	Fall'85	Spring'86	Breeding'86
Female	Control	18	12	8	7
	Fed	17	9	5	5
Male	Control	9	5	3	3
	Fed	7	4	2	2

b) JUVENILES:

Sex	Area	No. of individuals Recruited'85	Fall'85	Spring'86	Breeding'86
Female	Control	23	13	9	9
	Fed	26	15	13	13
Male	Control	17	9	4	3
	Fed	14	4	0	0

Table 19. a) Numbers and sex ratio of juveniles captured on fed and control areas during 1985 and 1986 (n=248). b) Data from a) re-classified into early- and late-season cohorts. Late-season juveniles were classified as those born more than 25 days after the first parturition on their natal area (see text for details).

a)	Area	Male	Female	Sex-ratio (% males)
1985	CONTROL	17	23	43%
	FED	14	26	35%
1986	CONTROL	34	29	54%
	FED	60	45	57%

b)	Season	Male	Female	Sex-ratio (% males)
1985	EARLY	19	33	37%
	LATE	12	16	43%
1986	EARLY	48	46	51%
	LATE	46	28	62%

FIGURE 8.

Seasonal changes in mean home range indices for overwintered residents (data for control and fed areas in 1985 and 1986 were pooled). A home range index was calculated for each individual that was live-trapped on 3 or more occasions. The index was calculated as the natural logarithm of the mean distance between locations of capture (see text for details). Means are presented ±1 standard error; sample sizes ranged from 24 to 40 for males, and 48 to 81 for females. Within-sex variances were homogeneous (F_{max} test; males $p>0.05$, females $p>0.05$).

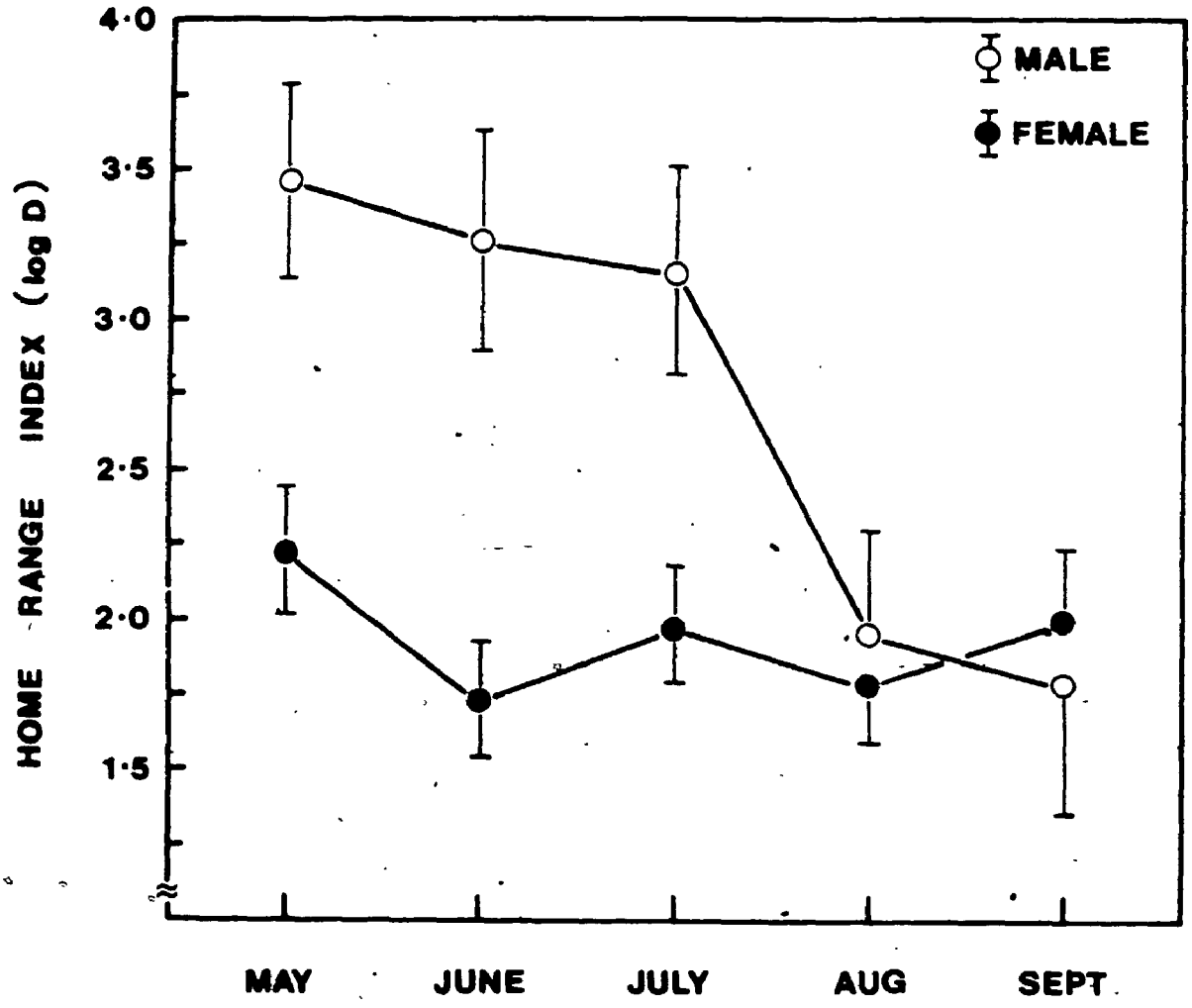

4·0
3·5
3·0
2·5
2·0
1·5
HOME RANGE INDEX (log D)
MALE
FEMALE
MAY
JUNE
JULY
AUG
SEPT

FIGURE 9.

Population trends on a) control areas, and b) fed areas, from August 1984 through September 1986. Supplemental food was continuously available on the fed areas from April 1985 through September 1986, although live-trapping was discontinued during each winter. Three control areas and 2 fed areas were not extensively trapped during August 1984, and were excluded from this comparison.

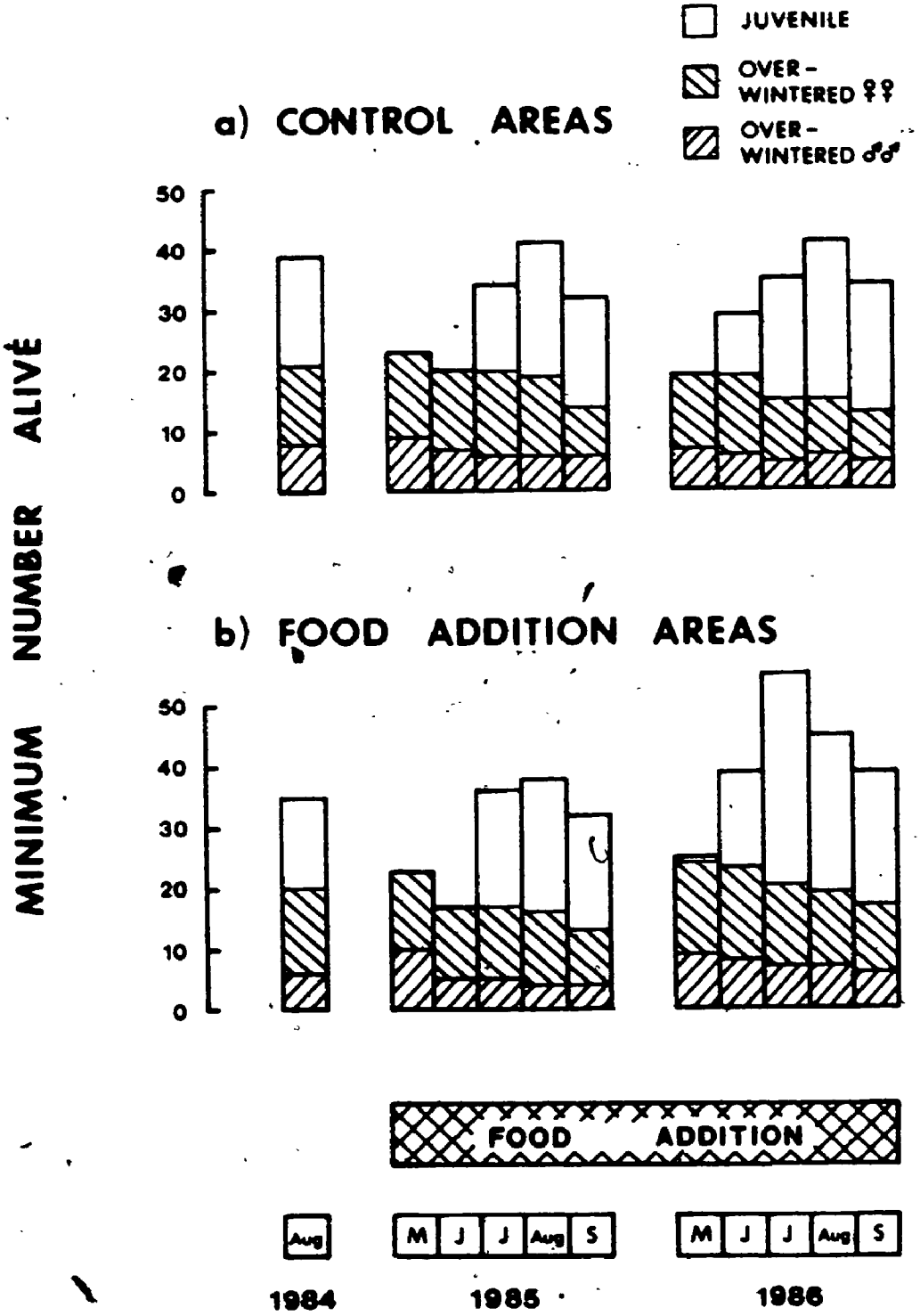
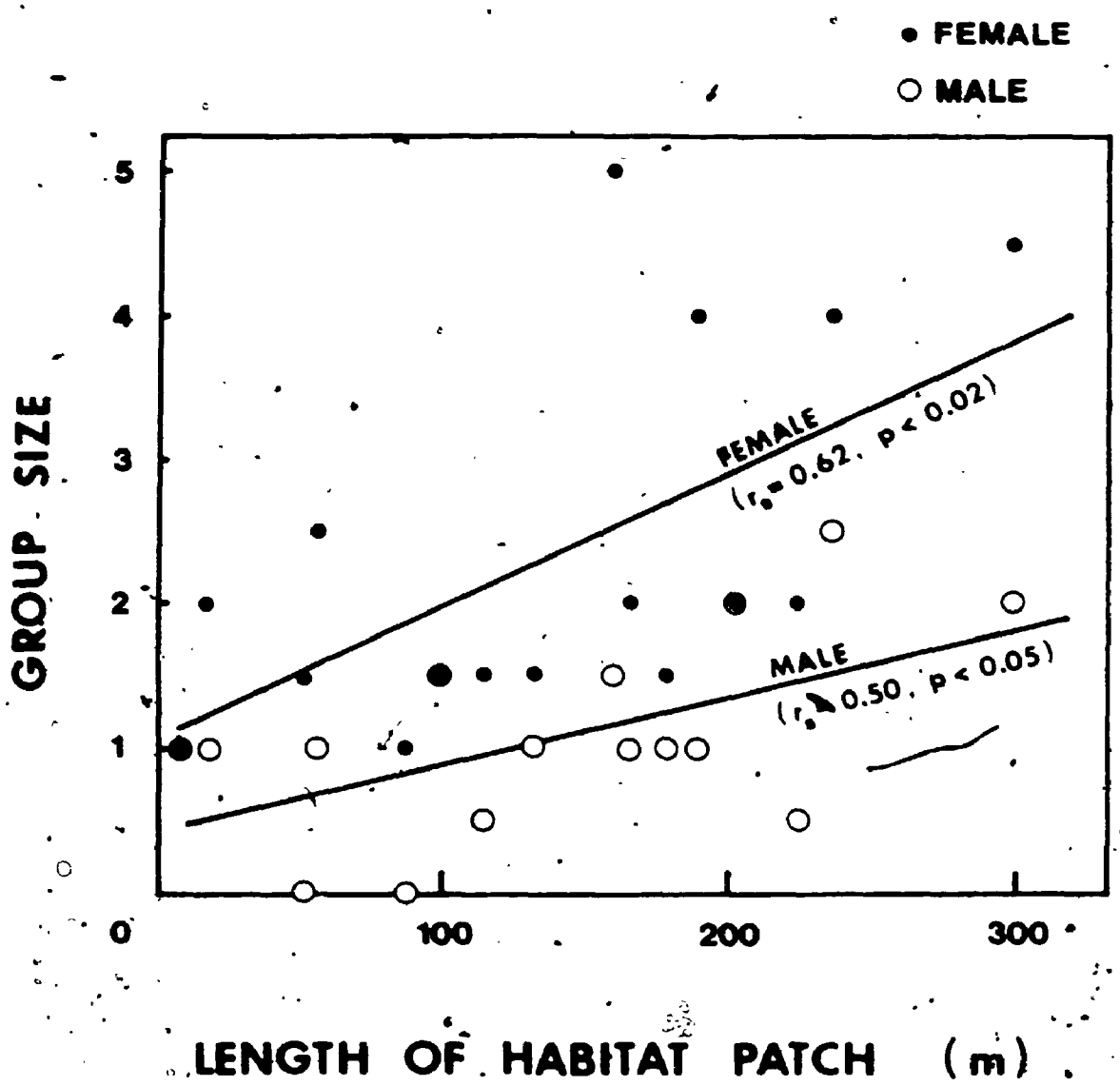

JUVENILE
OVER-WINTERED ♀♀
OVER-WINTERED ♂♂
a) CONTROL AREAS
b) FOOD ADDITION AREAS
MINIMUM NUMBER ALIVE
50
40
30
20
10
0
FOOD ADDITION
Aug
M J J Aug S
M J J Aug S
1984
1985
1986

FIGURE 10.

Relationship between size of habitat patch and mean numbers of resident male and female bushy-tails present during the 1985 and 1986 breeding seasons. Patch size was defined as the horizontal length of exposed rock, as measured from aerial photographs. Trend lines were calculated as the major axis for each bivariate sample (Sokal and Rohlf 1981:595). Coefficients are given for Spearman rank correlations. ● indicates that the numbers of males and females in a group were equal.


• FEMALE
○ MALE
GROUP SIZE
0
1
2
3
4
5
100
200
300
FEMALE
(r_s = 0.62, $P < 0.02$)
MALE
(r_s = 0.50, $P < 0.05$)
LENGTH OF HABITAT PATCH (m)

4.4. Discussion

Direct observation of social behaviour was not a practicable method for investigating the social organization of this nocturnal species. However, the basic structure of bushy-tail social organization was apparent from an analysis of the mark-recapture trapping data. Each overwintered female bushy-tail exhibited a close association with one patch of rocky habitat. Males also tended to be associated with a particular habitat patch, but their home ranges were larger than those of females during the breeding season. In addition, some males moved among adjacent patches of habitat.

The sex ratio of breeding residents was female-biased on the majority of areas during 1985 (69%) and 1986 (88%). Breeding resident males likely sired the offspring of females in their area because of their preferential, if not exclusive, access to these females. (Similar assumptions regarding paternity have been made in several field studies of Spermophilus and Ochotona populations e.g. McLean 1983; Murie and Harris 1978; Smith and Ivins 1983b). Thus, my results suggest that polygyny (sensu Wittenberger and Tilson 1980) was common in this population.

The social organization of bushy-tails in the Kananaskis Valley ranged from monogamy, through harem (uni-male) polygyny, to groups with 2 or more overwintered males and several overwintered females. The sex ratio of the groups varied between the 1985 and 1986 breeding seasons in the majority of areas. These results support the prediction that bushy-tails exhibit variable social organization. Monogamy was associated with small patches of habitat, whereas multi-male groups

occurred only on rock outcrops that had a horizontal length of at least 150 m. Thus, variation in social organization was related to the heterogeneous distribution of breeding habitat. This variation was consistent with the hypothesis that bushy-tails exhibit a mating system based on resource defence polygyny.

Several other studies have investigated intraspecific variation in mammalian social organization in relation to habitat heterogeneity. For example, Cowan and Garson (1985) found that patchy distribution of burrows in an area of hard substrate led to aggregation of female European rabbits (Oryctolagus cuniculus) and subsequent territorial defence of females by males. In a sandy area, the rabbit population was characterized by a dispersed distribution of females. Males in this area exhibited an opportunistic mating strategy whereby receptive females were guarded only during the brief period necessary for the male to obtain a successful copulation. Bush hyrax (Heterohyrax brucei) inhabit rock outcrops ("kopjes") in the Serengeti (Hoeck et al. 1982). Female group size in hyrax was positively correlated with kopje size. On large kopjes, groups of females were associated with a single territorial male and several peripheral males. Peripheral males harrassed the territorial male during courtship, and were sometimes able to copulate with females. On smaller kopjes, peripheral males were excluded by the territorial male, which thereby gained exclusive access to the resident females.

There was no evidence that food addition influenced the home range size of either male or female bushy-tails. Home range size of males varied seasonally, however, and was largest during the breeding season. This suggests that male ranging behaviour was primarily

related to competition for mates rather than for food. Similar results have been reported by Kenward (1985) who used radio-tracking in conjunction with a food addition experiment to investigate seasonal changes in the ranging behaviour of grey squirrels (Sciurus carolinensis). Grey squirrel home ranges were more clearly influenced by sexual activity than by proximate changes in food abundance. Male squirrels increased their home range markedly at the start of the breeding season, whereas female home range size varied little during the year and was not influenced by the addition of food during winter. Similar seasonal changes in male spacing behaviour have been reported for Tamias striatus (Ickes, in Mares et al. 1976), Peromyscus leucopus (Hansen and Batzli 1978), Mustela erminea (Sandell 1986), Tamiasciurus douglasii (Koford 1982; Smith 1968), and Sciurus aberti (Farentinos 1972).

During the breeding season, males of the above species may adopt a tactic of either territorial defence of breeding females, or non-territorial roaming in search of females (Erlinge and Sandell 1986). Both of these tactics (sensu Caro and Bateson 1986) were observed among male bushy-tails. Some males exhibited a close association with a single habitat patch, whereas others roamed among several adjacent patches during the breeding season. Escherich (1981:92) also noted that some males roamed among areas, but did not discuss this observation in relation to his suggestion that bushy-tails exhibit harem polygyny.

Sandell (1986) suggested that wide variation in social status would commonly favour the development of alternate mating tactics among males. If male status is closely linked to body weight (e.g.

Erlinge 1977), then weight-related differences could potentially outweigh any resident-intruder asymmetry in dominance status. This may allow large males to mate with the receptive females associated with smaller territorial males. If a male bushy-tail is large enough to be dominant over the majority of territorial males in a local population, then roaming may be his most profitable tactic for obtaining access to mates. Roaming would not be a profitable tactic, however, for a small male which was rarely successful in its attempts to intrude on other territories. A more profitable tactic for this male may be to remain closely associated with the females on his local area and to exclude other males from this area whenever possible. Observations of captive bushy-tails indicate that aggressive encounters between adults frequently escalate to the point at which serious wounding occurs (Escherich 1981; pers. obs.). In the field, roaming males exhibit a higher frequency of wounding than either local or transient males, which suggests that roamers are frequently involved in aggressive encounters with other individuals.

Transient bushy-tails were the smallest males in the local population and were likely subordinate to most other males. Woodrats use scent gland secretions to mark territorial boundaries (N. lepida: Vaughan and Schwartz 1980). During aggressive encounters between males, scent marking behaviour is primarily exhibited by the dominant individual (Howe 1977). Thus, the lack of scent gland activity among transient males suggests that these individuals had abandoned any attempt at establishing territories in favour of occupying peripheral habitat. Transients were usually yearlings and may, therefore, have become territorial during a subsequent breeding season.

Erlinge and Sandell (1986) suggested that male stoats (Mustela erminea) exhibit roaming behaviour as a response to the dispersed distribution of receptive females during the breeding season (the mean distance between breeding female stoats was about 1 km; Sandell 1986). The ability of a male to monopolize a group of females should increase as females become more closely grouped (Emlen and Oring 1977), and female bushy-tails exhibit a more aggregated distribution than do female stoats as a consequence of the patchy distribution of rocky habitat. Territoriality should, therefore, be relatively more successful for male bushy-tails than for male stoats. This prediction was supported by the observation that only 8 of 34 resident bushy-tails exhibited roaming behaviour, whereas roaming was the predominant strategy among male stoats (Sandell 1986).

I had expected that bushy-tails would usually form monogamous pairs on the smallest habitat patches, but monogamy during successive breeding seasons was observed in only 1 area. I suggest that the low frequency of monogamy in this population is related to the presence of roaming males. It may not be profitable (in terms of reproductive success) for a territorial male to defend an area occupied by a single female if there is a high probability of successful intrusion by a roaming male. A large territorial male may be able to prevent any such intrusions by roamers. However, this male would also be dominant over the majority of other territorial males and would, therefore, usually have the option of transferring from his monogamous situation to a habitat patch which would provide an opportunity for polygynous mating. The prediction that monogamous pairings are relatively unprofitable for territorial males was supported by the observation

that no resident male was present in 5 of the 10 cases where only 1 breeding female was recorded on a trapping area. Escherich (1981) reported a similar observation of a single female which bred on an area in the absence of a resident male.

Although roaming males moved among several habitat patches, they were primarily captured on one particular area, and they remained on this area once the breeding season had ended. This area was apparently the location of the den in which they overwintered. I speculate that these large males do not initiate roaming at the start of each breeding season until they have mated with the females on their local patch of habitat.

Multiple residency of males was observed on large rock outcrops. The nature of social interactions among these resident males is unclear. Intrasexual territoriality would be expected if male mating success is dependent on defence of resources (Emlen and Oring 1977), but live-trapping did not provide a readily interpretable measure of home range overlap. Bushy-tails exhibited a despotic form of social organization in captivity (Chapter 2), and Kinsey (1976) reported similar behaviour among low-density groups of N. floridana in captivity. These data provide some evidence that woodrats do not readily form non-territorial dominance hierarchies. Vaughan and Schwartz (1980) reported that N. lepida maintain territories with little overlap among individuals of the same sex, and a similar pattern of territoriality has been reported for N. stephensi (Ward 1984). Thus, resident male bushy-tails may coexist on large habitat patches by subdividing each patch into mutually exclusive territories.

Seasonal reduction in male home range size coincided with weaning

of the late-season cohort of juveniles (Chapter 3). Resident males may extend territoriality beyond the mating season to reduce the risk of intruding males being infanticidal towards nestlings (e.g. McLean 1983).

The other variable component of bushy-tail social organization was female group size. Part of this variation arose as a consequence of variation in the size of different habitat patches, since female group size was positively correlated with patch length. This correlation indicates that physical resources were important in determining group size. However, food, den sites and inter-individual spacing were all likely correlated with patch length. The relative importance of the latter two factors remains unclear.

Average per capita reproductive output of female bushy-tails declined as female group size increased. Similar trends in average reproductive success have been reported for yellow-bellied marmots (Marmota flaviventris: Downhower and Armitage 1971) and European rabbits (Oryctolagus cuniculus: Cowan and Garson 1985). Reduced reproductive output with increasing group size suggests that these species do not form female groups because of co-operative advantages to group membership. For these species, areas of suitable breeding habitat are relatively scarce (e.g. Svendsen 1974) and females which group on patches of high quality habitat are likely to have greater reproductive success than non-grouping females, despite the costs of competition that are associated with group formation.

Models relating polygyny in mammals to habitat quality (Orians 1969; Wittenberger 1980) usually assume that females are able to accurately assess the quality of each patch of habitat before deciding

where to settle (Vehrencamp and Bradbury 1984). This assumption is unlikely to be valid for bushy-tails and other species in which recruitment of females occurs primarily through natal philopatry. If there is considerable risk to dispersal, females should attempt to breed on their natal area rather than move to an unknown area (Hamilton and May 1977; Michener 1983). Female groups may consequently be larger than would be predicted by the theoretical models of Orians (1969) and Wittenberger (1980) because these models do not incorporate the risk associated with dispersal. A further consequence of natal philopatry is that a change in the level of a critical resource within a habitat patch may influence female group size by altering the level of competition among group members, whereas a change in relative resource abundance among habitat patches is unlikely to be detected by females.

Although the negative relationship between per capita reproductive success and female group size was more apparent on control areas than on fed areas (Chapter 3), the experimental addition of food provided no evidence that group size was influenced by food abundance. Food addition did increase reproductive output (Chapter 3), but the majority of juveniles captured on the trapping areas disappeared from their natal area before becoming reproductively mature. Significantly, food addition did not result in increased immigration of bushy-tails. Increased immigration has been an important componen of the population increases observed during several recent food addition experiments (Dobson and Kjelgaard 1985; Gilbert and Krebs 1981; Taitt and Krebs 1981; Young and Stout 1986).

The lack of any significant increase in the number of bushy-tails

on fed areas does not support the hypothesis that food acts as a proximate limit to group size in this species, and is contrary to the results of the majority of studies involving addition of food to small mammal populations (Boutin 1984; Dobson and Kjelgaard 1985). It could be argued that the absence of any population response to food addition indicated that bushy-tails did not utilize the supplemental food. However, it is clear that I used a suitable food supplement during this experiment, since reproduction and growth of bushy-tails varied significantly between fed and control areas. (The variables affected by food addition are summarized in Table 20).

Dobson and Kjelgaard (1985) provided supplemental food to populations of Columbian ground squirrels (Spermophilus columbianus) on a study area adjacent to the Kananaskis Valley. Ground squirrel population numbers increased by about 85% per annum on the fed areas during their study. Significantly, ground squirrels were observed to dig additional burrows during the population increase (Dobson, pers. comm.). In contrast, the option of increasing the number of den sites may not be available to bushy-tails, which den in rock crevices and caves. Thus, the number of available den sites was a potential limit to group size, as suggested by Escherich (1981) and Finley (1958). Nevertheless, bushy-tail group size varied between 1985 and 1986 on 12 of the 16 trapping areas. This suggests that the size of a bushy-tail group does not directly correspond with the number of den sites on a habitat patch.

Bushy-tails intensified their food hoarding behaviour during the fall (Appendix II) and increased their metabolic reserves during winter (Chapter 3). Despite these long-term adaptations to nutritional

stress during winter, I found that food addition did not influence the overwinter survival of bushy-tails. However, the 1985/86 winter was unusually mild (Chapter 3) and I speculate that survival differences would be observed between fed and control areas during a more severe winter.

Food addition did not influence the level of juvenile philopatry, which suggests that philopatry and dispersal were not directly related to competition for food. Bushy-tail dispersal was male biased, which is consistent with the hypothesis that competition among males for mating opportunities results in male biased dispersal in polygynous species (Dobson 1982; Moore and Ali 1984). In contrast to bushy-tails, pikas (Ochotona princeps) are found in patchy habitat but are monogamous (Smith and Ivins 1983b). Although recruitment of pikas into the breeding population occurs primarily through philopatry, there is no evidence of sex biased dispersal in this species (Smith and Ivins 1983b).

Johnson (1986) has extended Dobson's (1982) explanation for the association of polygyny and male biased dispersal by suggesting that males disperse more readily than females because they are better able to compensate for the energetic costs of dispersal. This asymmetry would arise if young males were prevented from breeding by the dominance of older males, whereas females bred as soon as they were physiologically mature. Thus, young males would pass through a period of reproductive inactivity, during which they would progressively gain in age- and weight-related social status. Johnson (1986) suggested that this gain in status would negate the initial energetic costs associated with dispersal. This explanation is consistent with my

observation that yearling females breed successfully, whereas the majority of yearling males have little opportunity to reproduce.

Juvenile male and female bushy-tails were never observed to be simultaneously philopatric in an area. Therefore, dispersal of juvenile bushy-tails reduced the probability of inbreeding (e.g. Packer 1985; Wolff and Lundy 1985). Mate competition and inbreeding avoidance need not be mutually exclusive explanations for dispersal in mammals (Dobson and Jones 1985).

The majority of juveniles (69%) disappeared from their natal area before the subsequent breeding season. Significantly, most of these non-philopatric juveniles (75% in 1985) had disappeared by mid-September, when food caching among the remaining bushy-tails began to intensify (Appendix II). Reduced group size during winter may lower the frequency of aggressive encounters necessary for resident individuals to defend their winter food caches against conspecifics. Thus, reduction in group size during late summer and early fall is likely adaptive for those individuals which remain on a habitat patch during winter.

I found that juvenile females born early in the breeding season were more likely to become resident on their natal area than those born late in the season. I suggest that disappearance of late season female juveniles is a result of competition among juveniles for suitable habitat. Late season juveniles are lighter than early season juveniles and relative weight is likely an important determinant of dominance during aggressive interactions (e.g. Erlinge 1977).

The proportion of weaned offspring that were male tended to increase during the breeding season. This seasonal trend in sex ratio

of offspring is not consistent with the hypothesis of local resource competition (Clark 1978; Silk 1983) which predicts that early season litters should be male biased so as to reduce the level of competition between reproducing adults and their philopatric female offspring. There was also no support for the prediction that females with large energy reserves invest preferentially in male offspring (Trivers and Willard 1973). Food addition resulted in increased body weight of breeding females (Chapter 3) but did not influence the sex ratio of their offspring. The seasonal increase in the proportion of male offspring did support the post-weaning investment hypothesis of Clutton-Brock and Albon (1982), which predicts that females bias their offspring sex ratio in favour of the more philopatric sex (females) during the period when these offspring would gain the greatest benefit (early in the season).

Other field studies have reported seasonal variation in sex ratio of offspring although their results are contradictory. Goundie and Vessey (1986) found that litters of Peromyscus maniculatus born in the spring were male biased while those born in the fall were female biased. As breeding females were heavier in spring than fall, these authors interpreted the seasonal decline in sex ratio as supporting the hypothesis that females with large energy reserves invest preferentially in male offspring (Trivers and Willard 1973). In contrast, Microtus pennsylvanicus exhibits a seasonal increase in offspring sex ratio (McShea and Madison 1986). Furthermore, heavy females of M. pennsylvanicus produce a higher proportion of female offspring during the fall than do light females, which is contrary to the predictions of Trivers and Willard (1973).

In 1985, the breeding season was short and the majority of breeding females produced only 1 litter. In contrast, a longer breeding season in 1986 allowed the majority of females to produce 2 litters. Second litters tended to be male biased, as discussed above, which may explain why a higher proportion of male offspring were produced in 1986 than in 1985. A difficulty with this explanation is that food addition increased the proportion of females having second litters (Chapter 3) but had no effect on the sex ratio of offspring. However, the observation by McShea and Madison (1986) that heavy females of M. pennsylvanicus tended to produce more female than male offspring in the fall, despite a overall trend for fall litters to be male biased, suggests that season and maternal body weight may have confounding effects on the sex ratio of offspring. This problem highlights the difficulties inherent in any attempt to demonstrate adaptive variation of sex ratio in mammals (Clutton-Brock and Iason 1986).

In summary, the results presented in this chapter are consistent with the hypothesis that bushy-tails exhibit resource defence polygyny. My second hypothesis, that supplemental food would increase female group size and the level of polygyny exhibited by territorial males, was not supported by the results of the food addition experiment.

Table 20. Summary of the influence of food addition through 2 successive breeding seasons on reproduction, growth, and group dynamics of bushy-tailed woodrats (Neotoma cinerea) in the Kananaskis Valley. 0 = no significant difference from control areas; + = significant increase relative to control areas ($p<0.05$).

Parameter			Response to food addition
Reproduction	-	initiation	earlier in season
	-	no. of litters	+
	-	litter size at weaning	+
	-	sex ratio of offspring	0
Post-weaning growth			+
Overwintered body weight			+
Home range			0
Group size			0
Group sex ratio			0
Immigration			0
Survival	-	adults	0
	-	juveniles	0

CHAPTER FIVE - CONCLUSIONS

The majority of field studies which have investigated the social organization of small mammals have involved relatively large, diurnal species (e.g. Murie and Michener 1984; Smith 1968; Smith and Ivins 1983b). These studies have generally been based on direct observation of individual behaviour. Less information is available on the social organization of small, nocturnal mammals due to the difficulty of monitoring their movements and social interactions. In contrast, demographic studies of small mammals have commonly involved nocturnal species (e.g. Microtus: Krebs 1985; Peromyscus: Taitt 1981). These latter studies have utilized mark-recapture trapping techniques or, less frequently, radio-tracking.

In this study, I have attempted to integrate information on i) the social organization of bushy-tails, and ii) demographic processes that occur at the level of the group, and which thereby affect the dynamics of the population as a whole. In taking this approach, I have incorporated difficulties inherent in both methods of study: individual behaviour could not be directly observed; movement patterns had to be inferred from mark-recapture trapping data; and sample sizes were relatively small. I suggest, however, that several characteristics of the bushy-tail population in the Kananaskis Valley were suited to a study of this nature. First, individual bushy-tails remained highly trappable through successive breeding seasons. A lifespan of several years, with continued growth as yearlings and adults, resulted in consistent, age- and size-related patterns of female reproduction and, apparently, male social status. In contrast,

small rodents such as Microtus and Peromyscus approach their asymptotic body mass during their first breeding season (Zullinger et al. 1984), and often do not survive long enough to breed during more than 1 year (e.g. Fairbairn 1976). Second, the patchy distribution of rocky habitat within the study area simplified the problem of discerning group structure from mark-recapture trapping data. For example, these discrete patches of habitat enabled me to view the ranging behaviour of males as a categorical reponse: males either did, or did not, roam among trapped areas. However, my assumptions regarding maternity and paternity of juveniles on the trapped areas must be treated with caution until more information becomes available.

It is useful to construct a system of classification which clarifies ecological and evolutionary relationships among the various social systems exhibited by related species (e.g. Crook et al. 1976; Emlen and Oring 1977). Ground-dwelling sciurids are one of the most studied groups of small mammals regarding their social organization, and Michener (1983) has proposed 5 grades of sociality for the North American representatives of this group: i) asocial ii) single-family kin clusters iii) female kin clusters with male territoriality iv) polygynous harems with male dominance, and v) egalitarian polygynous harems. A similar classification may be useful for other cricetid rodents, such as Neotoma. Escherich (1981) suggested that bushy-tails exhibited harem-polygyny, which would correspond to the fourth grade of ground squirrel sociality as typified by the yellow-bellied marmot (Marmota flaviventris: Downhower and Armitage 1971). However, given the variability of ranging behaviour among male bushy-tails, and the lack of conclusive evidence regarding the extent of male home range

overlap, I suggest that the basic unit of bushy-tail social organization should be compared with the third, rather than the fourth, grade of sociality listed above. The third grade is typified by the arctic ground squirrel (Spermophilus parryi: McLean 1982) and Columbian ground squirrel (S. columbianus: Murie and Harris 1978). Michener (1983) noted that the social organization of each of the above 3 species of ground squirrel corresponded to resource-defense polygyny as defined by Emlen and Oring (1977).

The social organization of a species is likely to influence many aspects of its population dynamics. Population regulation may commonly occur at the level of the group, rather than at the level of the population (Clutton-Brock and Albon 1985). Tamarin (1983) presented the following paradigm: "[small mammal] populations are regulated ultimately by a limiting resource(s), such as food, and proximately by their social behaviour and organization". Watson and Moss (1970) suggested criteria for determining whether or not a population was regulated by social factors: i) A substantial proportion of the population does not breed; ii) Non-breeders are physiologically competent to breed, and will do so if more dominant animals are removed; iii) The breeding animals are not using up some resource, such as food, space, or den sites - if a resource is depleted, it itself is limiting; iv) Behaviourally induced mortality is compensatory with other mortality factors. I have summarized below the data which my study provides to support the hypothesis that bushy-tail populations are limited by social interactions.

Necropsy of bushy-tails from a variety of habitats demonstrated that all overwintered females were physiologically capable of

breeding. Experimental addition of food demonstrated that survival rates, and the capacity to reproduce, were not directly limited by food (although reproductive output did vary in response to food). Den sites were a potentially limiting resource (Escherich 1981; Finley 1958), although it was unclear whether den availability could have directly limited the population since group size varied between 1985 and 1986 on the majority of trapping areas.

More than half of all juveniles weaned on the trapping areas disappeared before becoming reproductively mature. Disappearance was most common during the summer and early fall and was, therefore, unlikely to have been caused by thermoregulatory stress or starvation. I suggest that disappearance of juveniles during the summer and fall was the result of their dispersal from the natal area. If this interpretation is correct, then dispersal was associated with a considerable risk for females, since few females became resident on non-natal areas. If dispersal was a consequence of intraspecific competition (either for mates or for other resources) then dispersal was, in effect, a form of behaviourally induced mortality.

There was no direct evidence for compensatory mortality, other than the stability of population levels on fed and control areas among years. Population stability may have resulted from similar rates of reproductive output and mortality within each area during the period of study. However, reproductive output varied between 1985 and 1986 and was increased by the addition of food. It seems more likely that group size was controlled by changes in the relative proportion of juveniles which dispersed from, or remained philopatric on, their natal area.

These data provide partial support for the Watson and Moss (1970) criteria, and I conclude that social interactions were likely important in limiting the size of this population. Sinclair (1986) has argued, however, that the Watson and Moss criteria do not distinguish between the "self-regulation" and "resource-behaviour" hypotheses of population regulation. The self-regulation hypothesis (e.g. Chitty 1960; Tamarin 1983) suggests that intrinsic properties of individuals (such as behaviour, physiology, and genetic make-up) act as proximate limits to the size of animal populations, and that it is rare for individuals to become directly limited by resources. In contrast, the resource-behaviour hypothesis (e.g. Clutton-brock and Albon 1985; Haukioja et al. 1983; Watson and Moss 1970) suggests that populations are proximately limited by resources, and that the importance of social behaviour (such as territoriality or dominance hierarchy) lies in the role it plays in concentrating the effects of resource shortage on certain subordinate individuals within the population.

The results of this study do not allow me to reject either the self-regulation or resource-behaviour explanation for population regulation in this species. Social interactions may allow bushy-tail populations to be self-regulated at a size where no individuals experience a shortage of critical resources. More probably, the abundance of suitable denning sites on each habitat patch was a proximate limit to the size of the study population. The importance of social behaviour would then lie in determining which individuals were able to gain access to this critical resource. Thus, temporal variation in age- or weight-related social structure could result in variable group size being observed on habitat patches that had fixed

numbers of suitable den sites.

I conclude that bushy-tails exhibit a variable pattern of social organization, which is related to the heterogeneous distribution of their breeding habitat. The variable components of social organization in this species were male ranging behaviour and female group size. Food was a proximate limit to growth and reproduction, and consequently affected the relative reproductive success of individuals within each group of bushy-tails. However, the experimental addition of food demonstrated that the social organization of this species was not under the proximate control of food abundance during the period of study.

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APPENDIX I - TRAPPING AREAS

Information relating to the 16 control and fed trapping areas in the Kananaskis Valley is summarized in the table below.

Areas with resident populations of bushy-tails were identified by preliminary trapping during 1984 and ranked in pairs (RANK) by the maximum horizontal length (LGTH) of exposed rock visible on aerial photographs of each area. These ranks correspond to the numbers assigned to each area on the location map (Chapter 2; Figure 1). The Universal Transverse Mercator grid reference (GRID) provides location coordinates for each area which are accurate to within 100 m. These grid references correspond to Zone 11U on National Topographic System of Canada map No. 82J/14. The elevation of each area (ELEV) was determined from this topographic map. The distance between each area and the nearest adjacent patch of rocky habitat (DIST) was measured from aerial photographs. DIST values are marked with a (*) if the nearest adjacent habitat was regularly trapped during the study. The number of feeding stations (FSTN) is given for the 8 areas that were supplied with supplemental food during 1985 and 1986.

The physiography (PYSG) of each area was classified as follows: bluffs are steep, relatively continuous escarpments of exposed rock in the upper valleys; gorges are rock faces adjacent to creeks in the lower valleys; outcrops are discontinuous slabs of exposed rock in the mid and upper valleys; and talus are large boulder fields at a variety of elevations. The canopy vegetation (CAN) was classified as Absent (-); Pine (Pi); Spruce (Sp); or Aspen (Ap). The understory vegetation (UND) was classified as scrub (Sc); forbs (Fo); or grasses (Gr).

Vegetation plots were established in 5 areas to monitor seasonal changes in understory biomass; these areas are marked with a (#).

RANK	NAME	GRID	ELEV (m)	DIST (m)	LGTH (m)	FSTN	PYSG	CAN	UND
CONTROL AREAS:									
1	Lorette	475326	1600	290	8	-	Wooden bridge	-	Fo,Gr
2	Slippery	451326	1680	170*	56	-	Gorge/fallen logs	-	Sc,Fo
3	Sawmill	466291	1690	155*	88	-	Outcrops	Ap	Fo,Gr
4	Shady	568429	1560	320*	164	-	Outcrops/talus	Pi	Fo
5	Sibbald	567433	1540	320*	180	-	Outcrops/talus	Pi	Fo
6	Hidden	358288	1720	390	192	-	Outcrops	Pi	Fo
7	Marmot	466292	1660	90*	204	-	Bluff	Pi	Fo,Gr
8	Wedge	353291	1750	330	320	-	Bluff	Ap	Sc #
FED AREAS:									
1	Bridge	391312	1520	1920*	15	2	Concrete bridge	-	Gr
2	Castro	465294	1680	90*	52	2	Outcrop	Pi	Gr
3	Canyon	377326	1620	408	96	5	Gorge	Sp	Fo #
4	Chipmunk	350287	1680	380*	112	5	Outcrops	Pi	Fo
5	Nakiska	465293	1680	110*	132	8	Bluff	Ap	Fo,G #
6	Gulch	510358	1560	225*	160	10	Gorge/caves	Pi	Sc #
7	Pika	575431	1550	430*	228	10	Outcrops/talus	Pi	Fo,Gr#
8	Kel's	567414	1740	350*	236	12	Bluff	Pi	Sc

APPENDIX II - FOOD CACHING BEHAVIOUR

Caches of green vegetation and fungi were present in all bushy-tail dens that could be visually examined (n=17). It was not possible to estimate the total amount of stored vegetation because den entrances were generally too narrow to allow a complete inspection of their interior. Salt and Clarke (1979) reported that a bushy-tail food cache in a cabin in the upper Kananaskis Valley contained approximately 50 kg of stored vegetation.

Large caches of vegetation were rarely accumulated during summer. Small quantities of freshly collected material were often observed around den entrances during this season, but these were apparently eaten within hours or days of having been collected. A possible exception to this pattern arose from 3 records of relatively large amounts (2-5 kg) of freshly stored vegetation in the dens of lactating females. This vegetation had disappeared when I returned to the dens 3 weeks later, and I speculate that these exogenous food caches may function in a similar manner to endogenous fat reserves (Chapter 3) in helping to support the nutritional demands of lactation.

Food caching behaviour began to intensify during late August and September in both 1985 and 1986. Bushy-tails initially gathered vegetation onto exposed ledges around the den entrance. This vegetation had usually been moved back into the enclosed part of the den by the time an area was revisited. Pikas (Ochotona princeps) exhibit a similar seasonal pattern of haying behaviour (Conner 1983). Seasonal variation in food caching behaviour suggests that for both bushy-tails and pikas, this behaviour is primarily an adaptive

response to unpredictable food availability during winter, rather than a means of avoiding predation (cf. Formozov 1966).

To investigate the degree of selectivity exhibited by bushy-tails when they were caching plant material, I determined the species composition of 10 food caches during early September 1986. The table below lists the number of caches (out of a posible 10) in which a species comprised at least 10% of the total dry mass. The number of caches in which a species was the largest component of the total dry mass is given in parentheses. Plant species were identified from Moss (1983).

Species name	No. of caches	
Buffalo-berry (*Shepherdia canadensis* (L.) Nutt).	6	(4)
Milk mushroom (*Lactarius sp.*)	4	
Yellow hedysarum (*Hedysarum sulphurescens* Rydb.)	3	(2)
Northern bedstraw (*Galium boreale* L.)	3	
Prickly rose (*Rosa acicularis* Lindl.)	3	
Limber pine (*Pinus flexilis* James)	2	
Ground juniper (*Juniperus communis* L.)	2	
Willow (*Salix scouleriana* Barr. *ex* Hook.)	2	
Saskatoon-berry (*Amelanchier alnifolia* Nutt.)	1	(1)
Fireweed (*Epilobium angustifolium* L.)	1	(1)
Gooseberry (*Ribes sp.*)	1	(1)
Wild vetch (*Vicia americana* Muhl.)	1	(1)
Cut-leaved anemone (*Anemone multifida* Poir.)	1	

(cont.)

Species name (cont.)	No. of caches
Lindley's aster (Aster ciliolatus Lindl.)	1
Showy aster (Aster conspicuus Lindl.)	1
Dwarf birch (Betula pumila L.)	1
Purple clematis (Clematis occidentalis Hornem.)	1
Bunchberry (Cornus canadensis L.)	1
Pea vine (Lathyrus ochroleucus Hook.)	1
Trembling aspen (Populus tremuloides Mich.)	1
Choke cherry (Prunus virginiana L.)	1
White meadowsweet (Spiraea betulifolia Pallas)	1

REFERENCES:

Conner, D.A. 1983. Seasonal changes in activity patterns and the adaptive value of haying in pikas (Ochotona princeps). Can. J. Zool. 61: 411-416.

Formozov, A.N. 1966. Adaptive modifications of behaviour in mammals of the Eurasian steppes. J. Mammal. 47: 208-223.

Moss, E.H. 1983. Flora of Alberta. Univ. Toronto Press. Toronto. 687 pp.

Salt, J.R. and R. Clarke. 1979. Mammalian fauna of the Kananaskis Lakes, Upper Kananaskis River and Highwood Pass region, Alberta. Alberta Naturalist 9: 22-45.

APPENDIX III - FEMALE REPRODUCTION

A total of 36 overwintered females were classified as resident on the 16 control and fed trapping areas during 1985. Of these females, only 1 did not breed during 1985. Twenty-four of these resident females disappeared by the start of the 1986 breeding season and were replaced by 31 recruits. This resulted in a total of 43 overwintered females being present on the 16 areas during the 1986 breeding season. All resident females bred during 1986.

The table on the following page summarizes the number of breeding resident females (BFEM) on each area, the estimated number of litters produced on each area (LITT), and the estimated number of male and female offspring which were successfully weaned on each area (MJUV and FJUV, respectively). Estimates of the number of weaned offspring (total = 248) do not include 11 juveniles that were first captured more than 50 days after weaning; these were classified as probable immigrants. (Date of weaning was estimated from body weight at first capture, as described in Chapter 3).

	1985				1986			
	BFEM	LITT	FJUV	MJUV	BFEM	LITT	FJUV	MJUV
CONTROL AREAS								
1) Lorette	1	1	2	0	1	2	3	3
2) Slippery	2	2	2	0	3	5	2	3
3) Sawmill	1	2	2	3	1	2	2	4
4) Shady	1	1	3	0	3	3	0	2
5) Sibbald	1	1	2	1	2	2	3	4
6) Hidden	3	5	1	3	5	8	3	4
7) Marmot	4	6	8	4	4	8	10	8
8) Wedge	5	6	3	6	3	5	6	6
TOTAL	18	24	23	17	22	35	29	34
FED AREAS								
1) Bridge	1	2	3	1	3	6	8	10
2) Castro	1	1	1	2	2	4	2	5
3) Canyon	2	2	4	4	1	2	2	4
4) Chipmunk	1	1	2	2	2	4	8	10
5) Nakiska	1	2	5	2	2	3	6	5
6) Gulch	5	7	4	2	5	8	6	11
7) Pika	1	2	3	1	3	6	7	6
8) Kel's	5	6	4	0	3	5	6	9
TOTAL	18	23	26	14	21	38	45	60

APPENDIX IV - GROWTH ANALYSES

Coefficients are given on the following page for reduced major axis (RMA) linear regressions, and corresponding monomolecular growth equations, for growth data from free-ranging and captive juvenile bushy-tails. Juveniles weaned before July 1 were classified as spring-cohort; those weaned later were classified as summer-cohort. Captive juveniles were fed ad libitum. Weaning date for free-ranging juveniles was estimated from juvenile body weight at first capture, as described in Chapter 3.

RMA regression equations took the form:

$$\text{Weight}(T+21 \text{ days}) = B' + B'' \times \text{Weight}(T)$$

The sample size (n) and regresston coefficient (r^2) are given for each regression.

Monomolecular growth equations (after Ebert 1980) took the form:

$$\text{Weight}(t) = K(1 - e^{-bt})$$

$$\text{where: } b = -\log_e B''$$

$$K = B' / (1 - B'')$$

Regression equations were calculated separately for each cohort with the exception of summer males. The sample of weight increments for this group was small (n=7 for control areas, n=5 for fed areas) and the effect of food addition was non-significant within this sample (ANCOVA; F=0.69, p=0.42). Therefore, the data for summer males from fed and control areas were pooled during the analyses. Weight vs. age curves (Chapter 3) were plotted by assuming that body weight at weaning (23 days of age) was 92 g for females and 103 g for males.

Growth analyses were based on body weight increments over a 20-25

day interval. Some juveniles were not recaptured within this interval and were excluded from the analysis. Thus, sample sizes given below do not represent total numbers of juveniles within each cohort.

SEX	COHORT	RMA. REGRESSION B'	B	n	r^2	GROWTH EQUATION K	b
MALE	Spring - control	97	0.78	29	0.94	440	0.25
	Spring - fed	107	0.87	25	0.88	850	0.14
	Spring - captive	149	0.64	12	0.81	420	0.44
	Summer	84	0.73	12	0.65	310	0.31
FEMALE	Spring - control	91	0.66	42	0.85	270	0.42
	Spring - fed	97	0.72	42	0.93	340	0.33
	Spring - captive	102	0.63	12	0.95	280	0.46
	Summer - control	93	0.61	16	0.73	240	0.49
	Summer - fed	85	0.71	13	0.87	290	0.34

REFERENCE:

Ebert, T.A. 1980. Estimating parameters in a flexible growth equation, the Richards function. Can. J. Aquat. Sci. 37: 697-692.

APPENDIX V - LIFE HISTORY TRAITS

Life history parameters for bushy-tailed woodrats (Neotoma cinerea) in the Kananaskis Valley are summarized in the table below. Data from areas supplied with supplemental food were excluded from this summary. Data presented as: mean (range; sample size).

Trait	Male	Female
Adult weight (g):	419 (379-456; 17)	302 (234-359; 42)
Breeding by young of the year:	No	No
Overwintered residents in reproductive condition[a]:	100% (30)	97% - 100% (67)
No. of litters per female:	-	1.46 (1-2; 36)
Litter size:	-	3.42 (3-5; 26)
Gestation[b] (days):	-	27-32
Neonate weight (g):	15.0 ± 0.2 (12)	14.4 ± 0.2 (10)
Weaning weight in field[c] (g):	103 (94-109; 10)	92 (84-102; 10)
Weaning age in captivity[d] (days):	23 (22-26; 7)	As for male
Nestling survival to weaning:	60% (sexes not distinguished)	
Weanling survival[e] (yearly):	10% (31)	45% (49)
Adult survival (yearly):	31% (16)	34% (35)
Growth rate in field[f] ($g \cdot day^{-1}$):	3.0	2.6

a. Males with scrotal testes; females pregnant or lactating.

b. Egoscue (1962).

c. Mass at entry into trappable population.

d. Age at emergence from nest-box.

e. On natal area.

f. For first 30 days post-weaning.

APPENDIX VI - GROUP COMPOSITION

The composition of groups of bushy-tails on the 16 control and fed areas in the Kananaskis Valley during 1985 and 1986 is summarized on the following 2 pages. Group size (GS) was defined as the total number of breeding residents (BR) on each trapping area. Residents were defined as overwintered individuals that were live-trapped on an area at least 3 times and that had a trappability of at least 50%. Residents were classified as breeding if they were captured in reproductive condition before 1 July. (The mean date of last parturition for breeding females occurred during the the first week of July in both 1985 and 1986. Mean date of last parturition did not vary between control and fed areas; $t=0.09$, $p=0.9$). Non-resident bushy-tails were classified as transients (TR) unless they were known to be resident on another trapping area. These latter individuals were classified as roamers (RO).

1985:	GROUP SIZE	MALE BR	MALE RO	MALE TR	FEMALE BR	FEMALE RO	FEMALE TR
CONTROL AREAS:							
1) Lorette	2	1	-	-	1	-	1
2) Slippery	3	1	-	1	2	-	-
3) Sawmill	1	-	2	-	1	-	-
4) Shady	2	1	-	-	1	-	-
5) Sibbald	2	1	-	-	1	-	-
6) Hidden	4	1	1	1	3	-	2
7) Marmot	6	2	-	-	4	-	-
8) Wedge	7	2	-	1	5	-	1
TOTAL	27	9	3	3	18	0	4
FED AREAS:							
1) Bridge	2	1	-	-	1	-	1
2) Castro	1	-	1	-	1	-	-
3) Canyon	3	1	-	1	2	-	1
4) Chipmunk	1	-	1	1	1	-	1
5) Nakiska	2	1	-	-	1	-	1
6) Gulch	6	1	-	1	5	-	2
7) Pika	1	-	1	-	1	-	-
8) Kel's	8	3	-	1	5	-	1
TOTAL	24	7	3	4	17	0	7

1986:	GROUP SIZE	MALE BR	MALE RO	MALE TR	FEMALE BR	FEMALE RO	FEMALE TR
CONTROL AREAS:							
1) Lorette	2	1	-	-	1	-	1
2) Slippery	4	1	-	-	3	-	-
3) Sawmill	1	-	2	-	1	-	-
4) Shady	4	1	-	-	3	-	-
5) Sibbald	3	1	-	1	2	-	-
6) Hidden	6	1	-	2	5	-	-
7) Marmot	6	2	-	1	4	-	-
8) Wedge	5	2	-	1	3	-	1
TOTAL	31	9	2	5	22	0	2
FED AREAS:							
1) Bridge	4	1	-	1	3	-	1
2) Castro	2	-	1	-	2	1	-
3) Canyon	3	2	-	1	1	-	-
4) Chipmunk	3	1	-	1	2	-	1
5) Nakiska	3	1	-	1	2	-	-
6) Gulch	7	2	-	-	5	-	-
7) Pika	4	1	-	-	3	-	-
8) Kel's	5	2	1	-	3	-	1
TOTAL	31	10	2	4	21	1	3